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William T. Stanley

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Cover: Four vertebrates found in montane habitats of Tanzania: *Sylvisorex howelli* (top left, photo by W. Stanley); *Praomys delectorum* (bottom right, photo by W. Stanley); *Rhampholeon beraduccii* (top right, photo by M. Menegon); *Leptopelis* cf. *parkeri* (bottom left, photo by M. Menegon).

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Studies of Montane Vertebrates of Tanzania

Editor,
William T. Stanley

Department of Zoology
Field Museum of Natural History
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Preface

This volume presents papers on various mammalian and herpetological groups occurring on different Tanzanian mountains (Fig. 1) that have been the subject of faunal surveys over the past two decades. The geologic history of Tanzania is complex and dynamic. Consisting of ancient fault-block crystalline mountains that began forming more than 200 million years ago (the Eastern Arc Mountains) and volcanoes of 1 million years old, or younger, these isolated montane islands that span the country are home to many unique plants and animals. In some cases, these organisms are restricted to a single forest on one mountain.

The articles in this volume document select aspects of the natural history and systematics of the amphibians, reptiles, and small mammals of these unique Tanzanian montane habitats and provide insight into the ecology and relationships of these creatures. The information presented here also provides the means to help conserve these highly threatened montane forests. The baseline data generated by the faunal inventories discussed herein will be invaluable in measuring the effect of climate change, increased logging activity, or the expansion of human settlements in the various studied forests.

The first four chapters cover the "small mammals": shrews, bats, and rodents, of the Usambara Mountains, arguably the most famous of the Eastern Arc Mountains. The remaining five chapters report on the herpetological faunas of both Eastern Arc Mountains and western Tanzanian massifs associated with the Albertine Rift. All chapters herein are based on voucher specimens housed at the Field Museum of Natural History, Chicago; The Natural History Museum (ex. British Museum [Natural History]), London; the University of Dar es Salaam, Tanzania; and other vertebrate museum collections. These specimens are the point of reference to describe taxa, confirm identifications, and document reproductive condition and different ecological parameters that these chapters summarize. Voucher specimens address a basic tenet of the scientific method, in that they allow subsequent researchers to replicate results.

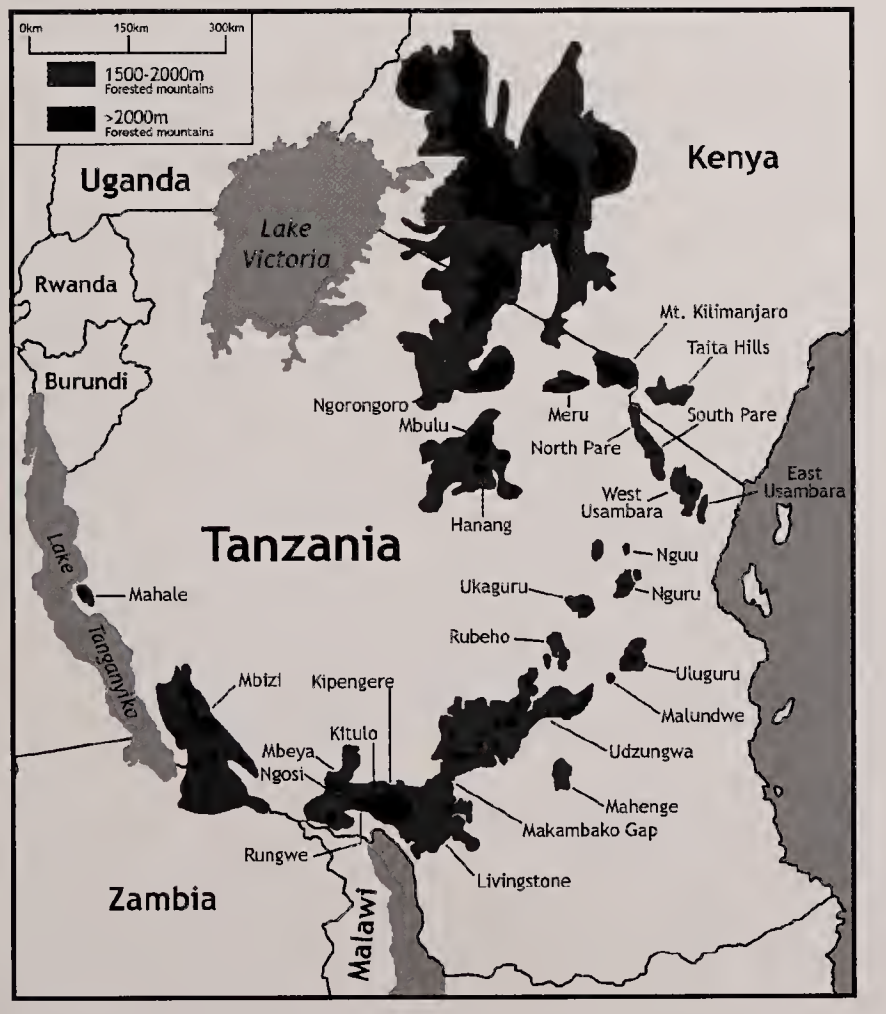

FIG. 1. Mountains of Tanzania.

FIG. 2. Dr. Kim M. Howell (center) during a field survey of the Uluguru Mountains in 1996. Dr. Charles Msuya is left, and Philip Kihaule is right.

This volume was conceived while Michele Menegon was driving me to the Julius Nyerere International Airport on a humid September night in 2008. While my good friend was worrying about the increasing traffic in Dar, my thoughts wandered to the last call I had to make before boarding the plane. I needed to thank Dr. Kim M. Howell.

Dr. Howell (Fig. 2) is arguably the world's expert on Tanzanian herptofauna but is also well versed in many different aspects of the country's biota. His PhD thesis was on bats, he consults on the effects of the pet trade on Tanzanian birds, and he has advised myriad projects on coastal coral reefs. However, it is Kim's tireless support of students and researchers of all nationalities that sets him apart from many biologists and natural historians exploring the biological diversity of eastern Africa. Ever polite, always welcoming, Professor Howell is THE person to seek out whether you are just starting a new research project, or you are established in the research or university community of eastern Africa. All of us owe Kim in many ways. A letter of introduction, crucial advice on which habitat to sample or what route to take, the most appropriate person to approach to advance a research agenda, or a strong cup of coffee ... Kim has provided all of these.

Simply put, none of the research associated with papers in this volume could have been accomplished without Kim's help, support, and friendship. Our understanding, appreciation, and conservation of the unique biota covered within this volume directly result from his insatiable curiosity and interest to advance science.

W. T. Stanley
January 2011
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Chapter 1

Small Mammal Inventories in the East and West Usambara Mountains, Tanzania. 1. Study Areas, Methodologies, and General Results

William T. Stanley[1], Steven M. Goodman[1], and William D. Newmark[2]

[1]*Department of Zoology, Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, IL 60605, USA*
[2]*Utah Museum of Natural History, University of Utah, Salt Lake City, UT 84112, USA*

Abstract

The Eastern Arc Mountains of southeastern Kenya and Tanzania hold a rich and unique biodiversity. The most celebrated of these mountains arc the East and West Usambaras. Although these massifs have been the subjects of biological study for over a century, little is known about the shrews, bats, and rodents occurring in the montane forests. Using pitfall buckets, small mammal traps, and mist-nets, between 1991 and 1993, we surveyed the small mammals in the Amani area in the East Usambara and Ambangulu area in the West Usambara to document the natural history of the local fauna. These surveys were conducted during the dry season annually between early July and early September.

In this chapter, we outline the study sites, methodologies, capture rates, and other trapping details. A total of 18,563 sample-nights was accrued over the three-year study, and on these two massifs, we documented 12 crocidurine shrew, one macroscelidid elephant shrew, 19 bat, and 14 rodent species. Species accumulation curves suggest that additional trapping effort may be required in the East Usambara Mountains to have a more eomplete view of the local small mammal fauna. There was no significant difference in the number of individuals captured or measures of species diversity in the pitfall and trap lines that were installed in the same location during the course of this study, suggesting that repeated sampling did not negatively affect the small mammal fauna of the study areas.

Introduction

The Eastern Arc Mountains (EAM), which extend from southern Kenya to southern Tanzania, have been the focus of field and systematic studies by biologists because of their extraordinary levels of endemism and diversity. Over the past eentury, workers have studied the flora and fauna of the 12 separate massifs or "montane islands" making up the archipelago. Biota studied include bryophytes (e.g., Pócs, 1975, 1985), angiosperms (e.g., Lovett et al., 1988; Lovett, 1990; Iversen, 1991; Cordeiro & Howe, 2003), invertebrates (e.g., Griswold, 1991; Hoffman, 1993), reptiles and amphibians (e.g., Loveridge, 1935, 1937; Menegon et al., 2008), birds (e.g., Stuart, 1983; Newmark, 1991, 2006; Cordeiro, 1998a; Lens et al., 2002), small mammals (e.g., Hutterer, 1986; Carleton & Stanley, 2005; Makundi et al., 2006; Stanley & Hutterer, 2007), and larger mammals such as primates (Davenport et al., 2006; Perkin, 2007; Rovero et al., 2009), carnivores (De Luca & Mpunga, 2005), and duikers (Rovero et al., 2005).

The Usambara Mountains in northeastern Tanzania, composed of separate eastern and western massifs, were among the first EAM studied and, as a result, are probably the best known of the archipelago. The village of Amani at about 900 m elevation in the East Usambara became in late 1800s the seasonal capitol of the German colonial government, bringing the area to the attention of naturalists, at least in part, with the installation of access roads and other infrastructure (Conte, 2004). The East African Agricultural Research Station and the National Institute for Malaria Research, both in Amani, attracted a numbcr of active field biologists, including Reginald E. Moreau, who documented the unique diversity of the area, with a focus on the forest-dwelling avifauna (Moreau, 1935). Although the forests in the Amani region have been under study for many years, little is known about certain biotic groups. This is particularly important in light of the local habitat alteration due to historical introduction of coffee (*Coffea arabica*) and tea (*Camellia sinensis*) plantations and small-scale agriculture over the last two centuries (Newmark, 2002) (Figs. 1 and 2). The discovery of gold in streams near Amani in 2003 has also caused a significant increase in human pressure on the forests over the last decade (Newmark, 2004).

The unusually high level of endemism exhibited by other biotic groups in the Usambara Mountains (Rodgers & Homewood, 1982), overlaid on largely datable patterns of natural forest fragmentation, prompted our study of the local small mammals. Between 1991 and 1993, we conducted three annual surveys of the small mammals (shrews, bats, rodents, and elephant shrews) in select forests of the East and West Usambara Mountains. The initial motivation for the surveys was to study the effect of forest fragmentation on small mammals using Newmark's (1991) research at the same sites on understory birds as the point of departure. Within this

FIG. 1. Tea plantations and forest on the Monga Tea Estate, East Usambara Mountains, Tanzania. Tea is planted in areas that were cleared of natural forest. Photo by W. T. Stanley.

FIG. 2. Agricultural area in the East Usambara Mountains resulting from human alteration of historically forested habitats. Note both tea plantation and areas cultivated for subsistence crops. Photo by W. D. Newmark.

chapter, we give details on previous small mammal studies conducted in the East and West Usambara Mountains, our study sites, sampling methodologies, and general results.

Previous Work

Given that Amani in the East Usambara and Lushoto in the West Usambara Mountains were administrative centers for the German colonial government of Tanganyika, the biological diversity of the surrounding forests has long been the subject of natural history studies (Rodgers & Homewood, 1982). Such investigations include those of Engler (1893, 1894) on plants, Barbour and Loveridge (1928) on terrestrial vertebrates, and Moreau (1935, 1952) on birds. The establishment of research stations focused on economic botany and disease vectors affecting humans attracted biologists to these massifs (Rodgers, 1998; Conte, 2004). In particular, the study of small mammal ectoparasites and their influence on human health has been on-going since the 1960s (e.g., Hubbard, 1972; Kilonzo et al., 1992, 2006).

Moreau (1935), in particular, highlighted the importance of the Usambaras as a center of biological diversity. Rodgers and Homewood (1982) summarized available information and presented faunal lists of various groups, including small mammals. Newmark (1991, 2006) and Newmark et al. (2010) studied the effects of forest fragmentation and disturbance on understory birds in the East and West Usambara Mountains. Although some taxonomic and plague vector studies previously focused on Usambara small mammals (e.g., Hutterer, 1986; Kilonzo et al., 1992), no intensive survey of shrews or rodents was conducted until the early 1990s, when this study was initiated. The organization Frontier-Tanzania (http://www.frontier.ac.uk/) conducted a series of faunal inventories, primarily in the East Usambara; the results are presented in technical reports (see Howard, 1996).

Conservation Actions in the East and West Usambara Mountains

Conservation efforts in the Usambaras were initiated more than a century ago under German colonial rule (Conte, 2004) and have increased in recent years. Reasons for conservation efforts include the importance of the Usambara forests as water catchments, the exceptional level of endemism among the plants and animals, and the historic human-induced habitat alteration, some of which started 2000 years ago in the Early Iron Age (Schmidt, 1989). The German administrators of Tanganyika, who recognized the value of the montane forests in northern Tanzania, including the East and West Usambaras, initiated the first documented large-scale conservation project. As a result, several forest reserves were established to protect water catchments, but also timber stands for later use by the colonial government (Rodgers, 1998). At the same time, the German colonialists created large agricultural estates in both the East and West Usambaras (Hamilton & Mwasha, 1989a; Conte, 2004).

After transitioning to British rule in 1916, a Forest Department was created in 1921 to expand timber exploitation. This new administration appreciated the importance of the local forests for soil and water conservation and created laws to reduce large-scale clearing of forests on private estates (Hamilton & Mwasha, 1989b). After Tanzania's independence in 1961, some reserves were partially de-gazetted and became sites for local agriculture, and the pressure on remaining forests increased dramatically (Hamilton & Mwasha, 1989c), as did calls for conservation of various natural habitats of the East and West Usambara Mountains (Redhead, 1981; Rodgers & Homewood, 1982). Many of the reviews summarizing the threats facing the forests of the Usambara Mountains list the critical need for biotic inventories to assist in developing conservation strategies (Rodgers & Homewood, 1982; Howell, 1989; Goodman et al., 1995).

Study Area

The East and West Usambara Mountains are within the Tanga Region administrative zone and separated by the Lwengera Valley, which descends to 300 m (Figs. 3–5). The West Usambara massif extends from approximately 4°28′ to 5°6′S and 38°10′ to 38°40′E. The East Usambara massif occurs from about 4°46′ to 5°13′S and 38°32′ to 38°50′E. This

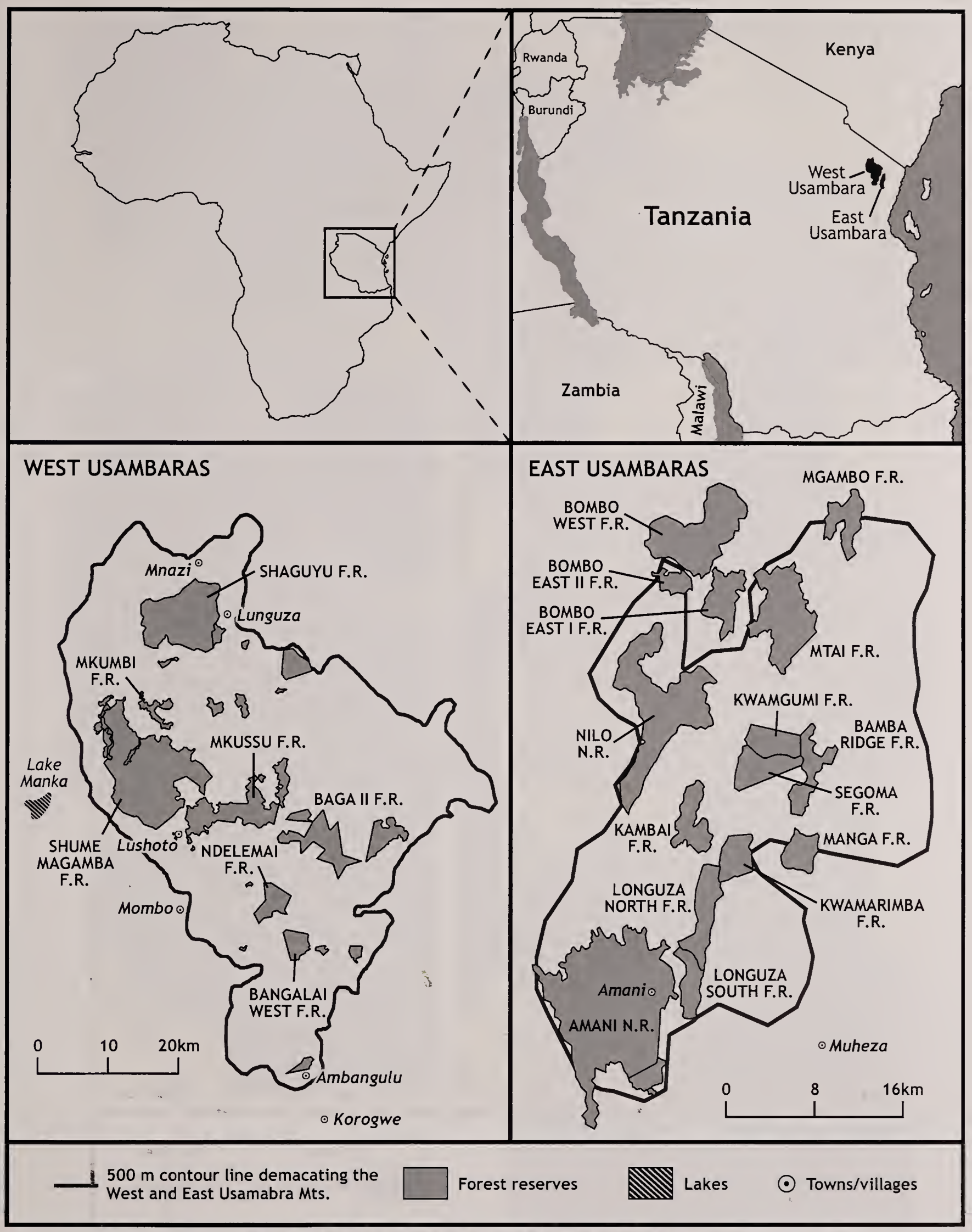


FIG. 3. General map of the East and West Usambara Mountains.

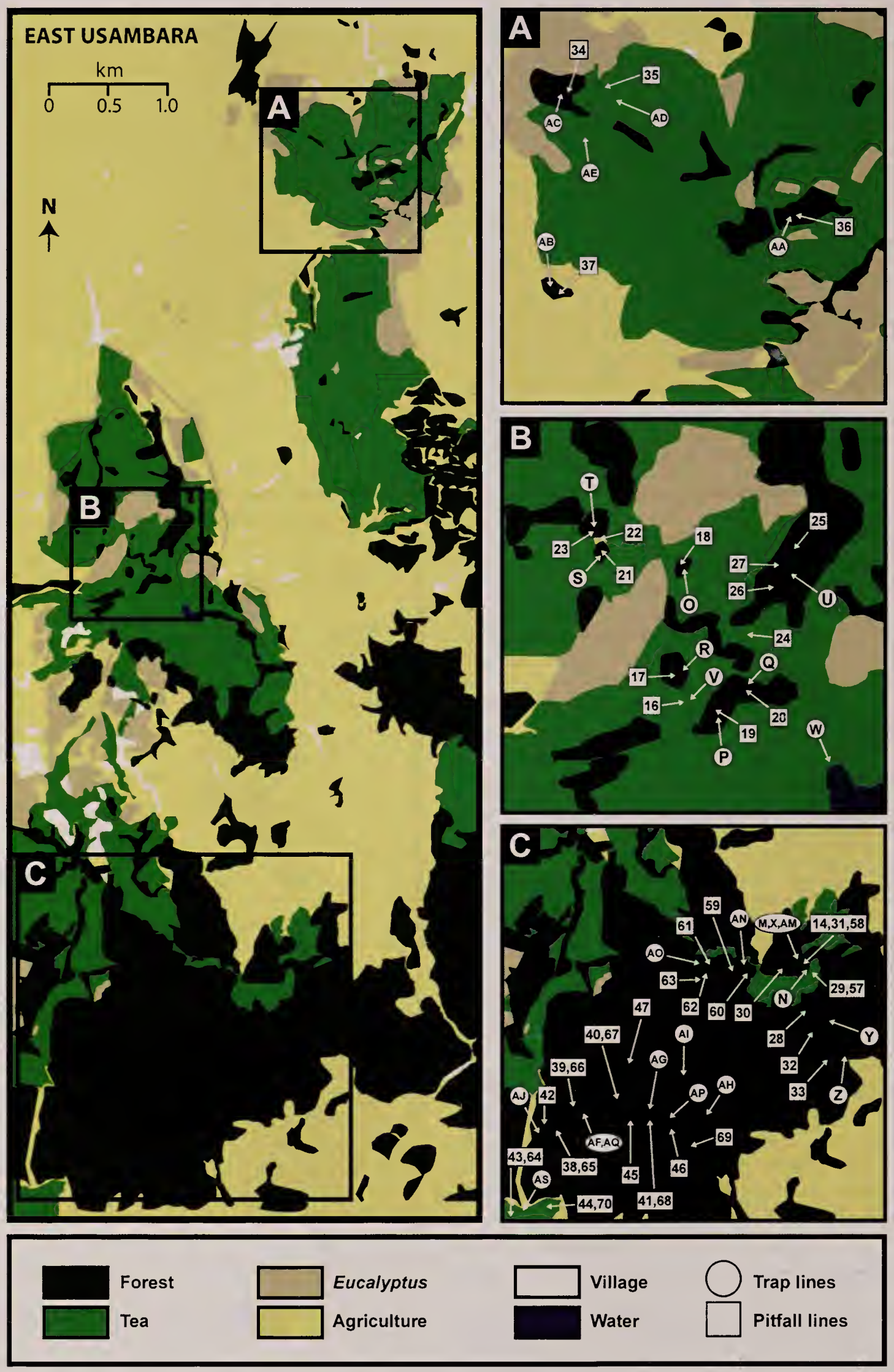
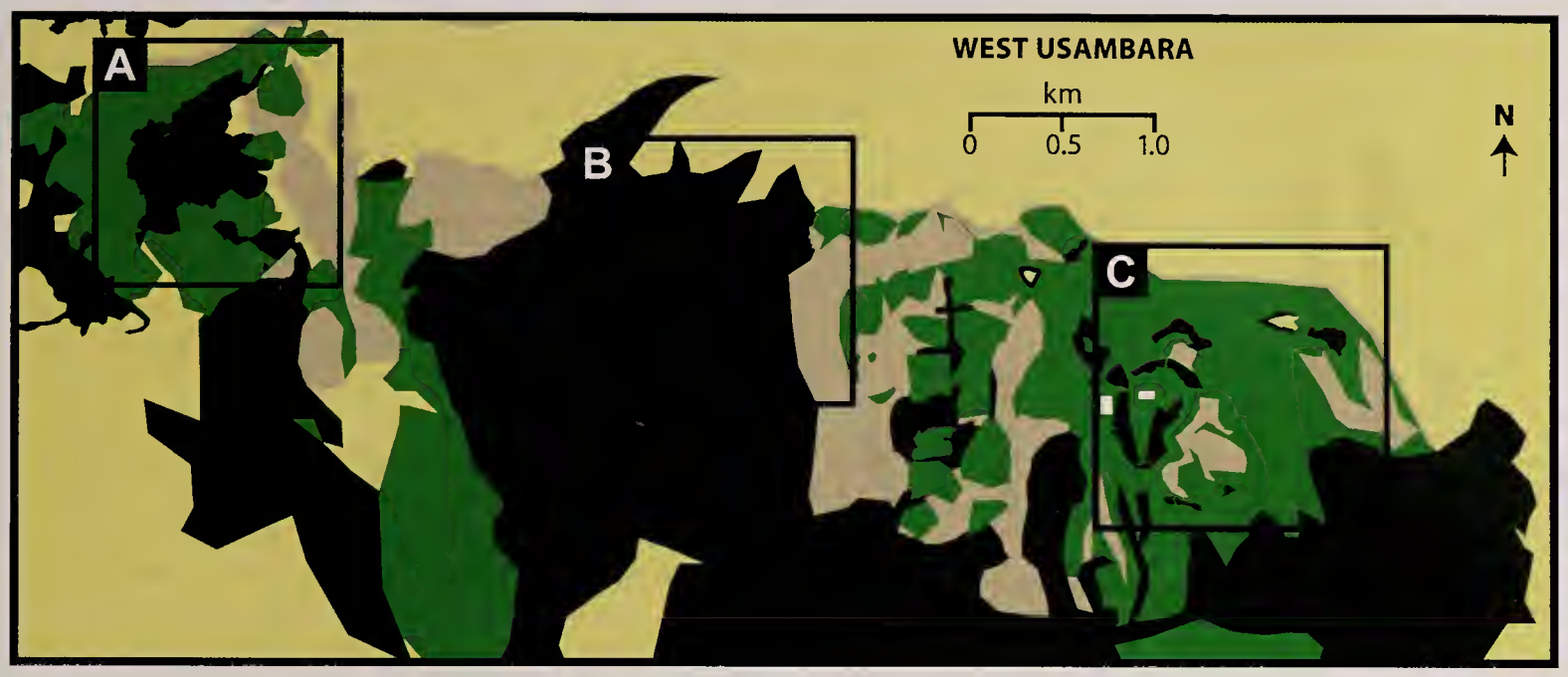
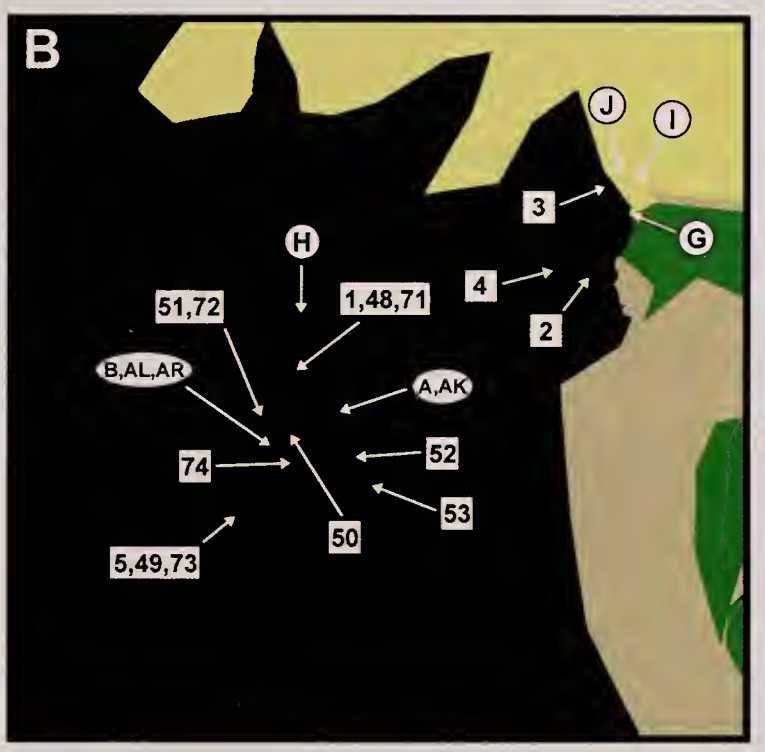


FIG. 4. Map of East Usambara study sites. Numbered circles refer to specific trap lines, and numbered squares refer to specific pitfall lines (see Tables 4 and 5).





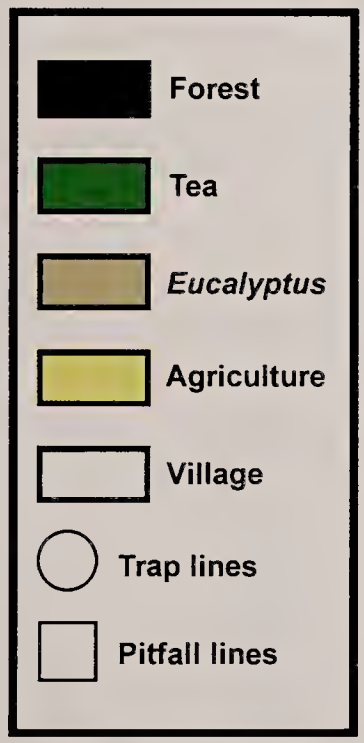


FIG. 5. Map of West Usambara study sites. Numbered circles refer to specific trap lines, and numbered squares refer to specific pitfall lines (see Tables 4 and 5).

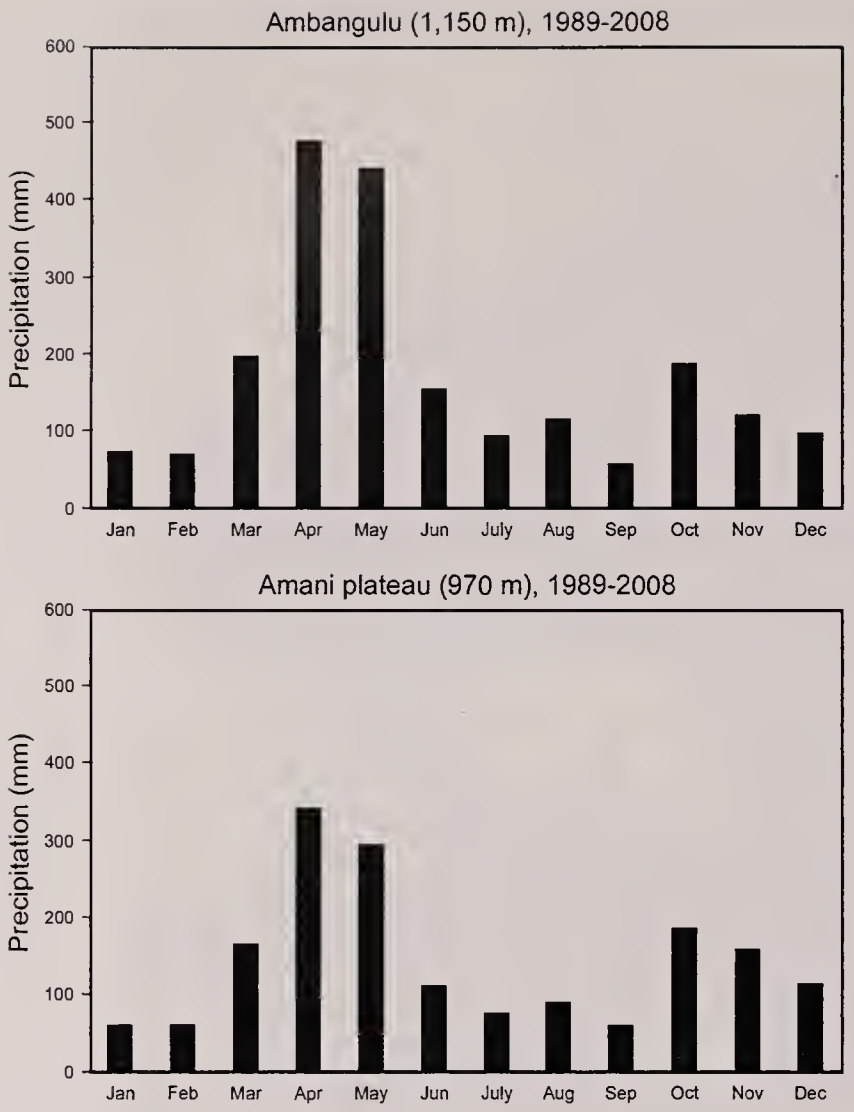


FIG. 6. Mean monthly precipitation between 1989 and 2008 at (**A**) 1150 m elevation at Ambangulu, West Usambara Mountains, and at (**B**) 970 m elevation at Marikitanda on the Amani Plateau, East Usambara Mountains.

study was conducted between 1991 and 1993 during the dry season. Natural forest, tree plantations, and non-forested matrix habitats comprising mostly tea or a combination of tea, *Eucalyptus,* and agricultural land were sampled on the Bulwa, Kwamkoro, and Monga Tea Estates and the Amani Nature Reserve in the East Usambara and on the Ambangulu Tea Estate in the West Usambara. Survey dates in the East Usambara were: 5–9 August 1991, 19 July–24 August 1992, and 30 July–13 August 1993. The Ambangulu Tea Estate forests in the West Usambara were sampled 1–31 July 1991, 27 August–4 September 1992, and 18–22 August 1993.

Moreau (1935) summarized the rainfall pattern across the East and West Usambara Mountains, based on records from regional meteorological stations, and found that areas near Amani in the East Usambara received the highest annual rainfall. Maximum annual rainfall in the West Usambara is along the southeastern edge of the massif. Based on long-term precipitation records recorded by the Marikitanda Tea Research Station (970 m) on the Amani Plateau in the East Usambara and the Ambangulu Tea Estate (1150 m) in the West Usambara, mean annual precipitation between 1989 and 2008 in the East Usambara was 1717 mm compared with 2056 mm in the West Usambara. Patterns of mean monthly precipitation over this period were very similar between the two weather stations (Fig. 6), although Ambangulu received on average 30% more precipitation during the "long rains" between March and June than Marikitanda. On the Amani Plateau, mean monthly temperatures recorded at 911 m from 1941 to 1970 ranged from 16.3°C to 24.8°C (Rodgers & Homewood, 1982). Although long-term temperature data are not available from Ambangulu, the simultaneous recording of air temperature at two-hour intervals in the control sites (see below) at Ambangulu and Amani over a 229-day period between November 1997 and July 1998 revealed that mean daily temperature is 1.6°C cooler at Ambangulu at 1250 m than at Amani at 977 m (Newmark, 2005). Thus, our study zone in the West Usambara is wetter and cooler than that of the East Usambara.

Sampling Sites

Details on forest sites, specific localities, sampling dates, and effort are listed in Tables 1 through 5, and mapped in Figures 4 and 5. The forested sites are fragments of

TABLE 1. Forest fragments sampled in the East and West Usambara Mountains between 1991 and 1993. Area (ha), W.D.N. study site(s) ID number, latitude and longitude coordinates, and elevation are presented for each study site. For further reference, site names used in the field notes of W.T.S. and S.M.G., as well as references to each fragment name as presented by Newmark (1991), are listed.

Forest fragment location	Area (ha)	W.D.N. site ID number	Coordinates	Elevation (m)	Site ID name in W.T.S./S.M.G. field notes	Fragment label in Newmark (1991)
East Usambara						
Bulwa fragments	2.6	5	5°1′37.78″S, 38°37′2.39″E	1042	2.7	1
	3.1	4	5°1′45.58″S, 38°37′27.49″E	972	1.6	2
	0.4	6	5°2′10.82″S, 38°36′48.38″E	982	0.38	3
Monga fragments	0.2A	9	5°3′33.78″S, 38°36′12.7″E	1136	0.1	4
	0.2B	13	5°3′28.63″S, 38°36′3.03″E	1137	0.42	5
	0.8	14	5°3′34.3″S, 38°36′3.18″E	1125	0.8	6
	29.4	10, 11, 12	5°3′25.34″S, 38°36′18.1″E	1057	30	7
	0.6	8	5°3′43.75″S, 38°36′10.23″E	1150	0.45	8
	3.3	7	5°3′47.69″S, 38°36′14.38″E	1141	9.4	9
Amani Nature Reserve	521	3, 16, 17	5°6′21.43″S, 38°35′52.07″E; 5°5′41.19″S, 38°37′7.32″E	1057	EU Control	10
West Usambara						
Ambangulu	886	22, 23	5°4′0.45″S, 38°24′37.71″E	1297	WU Control	
	37.8	21	5°3′40.1″S, 38°23′163″E	1215	40	
	5.5	18	5°4′20.41″S, 38°25′44.59″E	1179	2.4	
	1.9	20	5°3′57.59″S, 38°26′2.73″E	1171	1.8	
	1.5	19	5°4′3.54″S, 38°25′49.28″E	1191	0.8	

TABLE 2. Sampling effort across all three years for both the East and West Usambara Mountains. Sample-nights represent the sum of bucket-nights and trap-nights.

	1991			1992			1993			Total		
Massif	Bucket-nights	Trap-nights	Sample-nights	Bucket-nights	Trap-nights	Sample-nights	Bucket-nights	Trap-nights	Sample-nights	Bucket-nights	Trap-nights	Sample-nights
East Usambara	66	410	476	2335	5917	8252	913	1698	2611	3314	8025	11,339
West Usambara	1058	4155	5213	607	905	1512	259	240	499	1924	5300	7224
Total	1124	4565	5689	2942	6822	9764	1172	1938	3110	5238	13,325	18,563

historically contiguous forest and were the same ones studied by W.D.N. (Newmark, 1991, 2006). In the East Usambara, 10 forest fragments were sampled, as well as non-forested habitats including tea, *Eucalyptus* plantations, and fallow agricultural land. Nine of these fragments were less than 30 ha; three were on the Bulwa Tea Estate, five were on the Monga Tea Estate, and one was on the Amani Nature Reserve. The smaller forest fragments ranged in size from 0.2 to 29.4 ha, whereas the biggest was 521 ha (Fig. 4). In the West Usambara, five forest fragments were sampled, including four smaller forest fragments ranging in size from 1.5 to 38.4 ha and a larger area that was 887 ha (Fig. 5). In this and subsequent chapters in this volume on mammals (Stanley & Goodman, this volume a,b; Stanley et al., this volume), we refer to each smaller fragment by its size (i.e., 29.4-ha fragment) and to the control sites in the East and West Usambara Mountains as the EU control site and WU control site, respectively. In the EU control site, the northeastern and southwestern portions were sampled during our small mammal surveys.

Field Methodology

PITFALL LINES—Small mammals were sampled using a variety of techniques. Pitfall lines were intended principally to capture shrews and, in most cases, were placed on narrow (<50 cm) trails cut for their installation. Each pitfall line consisted of 11 buckets, set 5 m apart, and buried in the ground with the top of the bucket flush with the ground. Each bucket was 26 cm high, with an upper diameter of 26 cm, a lower diameter of 24 cm, and a 15-liter capacity. The bottoms of the buckets were pierced with small holes to allow water drainage. Each line had a 50 cm-high opaque black plastic drift fence running over the center of each bucket (Fig. 7). These passive and non-baited traps capture animals moving on the forest floor that encounter the drift fence and follow it until they fall into a bucket. The pitfall lines were generally set along straight trails; however, rocks and logs occasionally forced deviations. For further details on this technique, see Stanley et al. (1996) and Voss and Emmons (1996). Pitfall lines were checked twice per day, in the early morning and mid-afternoon. A "bucket-night" refers to one bucket in operation for a 24-hour period (0700 to 0700 h). Table 4 lists each line with placement details.

TRAP LINES—Trap lines consisted of three different types of traps: Museum Specials, 14 × 7 cm; Victor Rat Traps (referred to as Victor Trap throughout this volume), 17.5 × 8.5 cm; and

TABLE 3. Sampling effort across all three years for both the East and West Usambara Mountains broken down by fragments and habitat types. Sample-nights represent the sum of bucket-nights and trap-nights.

	Bucket-nights	Trap-nights	Sample-nights
Forest habitats on each massif			
East Usambara			
Control site	1793	5690	7483
Fragments	792	2305	3097
West Usambara			
Control site	1397	2122	3519
Fragments	450	1560	2010
Non-forest habitats on both massifs			
Tea	575	1003	1578
Agriculture	154	470	624
Eucalyptus	77	175	252
Total	5238	13,325	18,563

FIG. 7. A section of a pitfall line utilized to catch shrews and small rodents. Note the plastic fence running transversely across the top of a bucket buried in the soil. Photo by W. T. Stanley.

TABLE 4. Summary of pitfall lines installed at different sites in the East and West Usambara Mountains between 1991 and 1993. Pitfall lines are listed by name (used in W.T.S. and S.M.G. field notes) in the first column, together with any lines that were set in the exact same location in other years. Also presented are the dates each pitfall line was in place and habitat type (F = forest, D = disturbed forest, A = agricultural land, T = tea) and site for habitats of forest and disturbed forest (see Table 1). Overall pitfall success includes both rodent and shrew captures.

Pitfall line/subsequent lines in same location	Dates and habitat (site)	No. of buckets/ bucket-nights	No. of species/no. of individuals (overall trap success [%])	No. of shrew species/no. of shrews (shrew trap success [%])	Coordinates
West Usambaras					
1991					
1/48, 71	1–10 Jul F (control)	12/108	3/10 (9.3)	3/10 (9.3)	5°40′3.22″S, 38°24′40.32″E
2	2–10 Jul F (control)	12/89	2/2 (2.2)	2/2 (2.2)	5°3′46.64″S, 38°24′42.54″E
3	5–13 Jul F (control)	11/88	3/4 (4.5)	2/3 (3.4)	5°3′38.56″S, 38°24′44.40″E
4	6–15 Jul F (control)	11/99	1/1 (1.0)	0	5°3′44.38″S, 38°24′40.57″E
5/49, 73	10–17 Jul F (control)	21/147	3/13 (8.8)	3/13 (8.8)	5°4′02.63″S, 38°24′37.24″E
6	17–24 Jul F (control)	11/77	0	0	5°3′40.41″S, 38°22′54.56″E
7	18–24 Jul F (control)	11/66	1/1 (1.5)	1/1 (1.5)	5°3′28.45″S, 38°22′59.89″E
8	20–24 Jul F/T (control)	8/32	2/2 (6.3)	2/2 (6.3)	5°3′37.95″S, 38°22′57.60″E
9	20–24 Jul D (control)	11/44	0	0	5°3′27.42″S, 38°23′13.57″E
10	13–17 Jul D (control)	11/77	4/7 (9.1)	2/5 (6.5)	5°4′22.99″S, 38°25′48.93″E
11	25 Jul–1Aug F (5.5)	11/77	0	0	5°4′20.85″S, 38°25′44.59″E
12	25 Jul–1Aug F (1.5)	11/77	1/1 (1.3)	1/1 (1.3)	5°4′08.54″S, 38°25′49.37″E
13	25 Jul–1Aug F (1.9)	11/77	2/4 (5.2)	2/4 (5.2)	5°4′01.84″S, 38°26′13.56″E
1992					
48/1, 71	27 Aug–5 Sep F (control)	11/99	2/5 (5.1)	2/5 (5.1)	5°4′03.22″S, 38°24′40.32″E
49/5, 73	27 Aug–5 Sep F (control)	21/189	2/8 (4.2)	2/8 (4.2)	5°4′02.63″S, 38°24′37.24″E
50	28 Aug–5 Sep F (control)	11/88	1/11 (12.5)	1/11 (12.5)	
51/72	28 Aug–5 Sep F (control)	11/88	1/9 (10.2)	1/9 (10.2)	
52	28 Aug–5 Sep F (control)	11/88	1/8 (9.1)	1/8 (9.1)	
53	31 Aug–5 Sep F (control)	11/55	2/2 (3.6)	2/2 (3.6)	
1993					
71/1, 48	18–23 Jul F (control)	11/55	1/3 (5.5)	1/3 (5.5)	
72/51	18–23 Jul F (control)	11/55	1/6 (10.9)	1/6 (10.9)	
73/5, 49	18–23 Jul F (control)	21/105	2/8 (7.6)	2/8 (7.6)	5°4′02.63″S, 38°24′37.24″E
74	19–23 Jul F (control)	11/44	1/6 (13.6)	1/6 (13.6)	
East Usambaras					
1991					
14/31, 58	5–11 Aug F (control)	11/66	2/4 (6.1)	2/4 (6.1)	5°5′37.28″S, 38°36′54.27″E
1992					
Monga					
16	18–26 Jul T	21/168	4/20 (11.9)	2/10 (6.0)	5°3′47.27″S, 38°36′11.53″E
17	19–24 Jul F (0.6 ha)	11/55	1/5 (9.1)	1/5 (9.1)	5°3′45.47″S, 38°36′10.46″E
18	19–24 Jul F (0.2A ha)	11/55	2/2 (3.6)	2/2 (3.6)	5°3′33.96″S, 38°36′11.72″E
19	19–24 Jul F (3.3 ha)	11/55	3/6 (10.9)	3/6 (10.9)	5°3′47.21″S, 38°36′15.21″E
20	19–24 Jul F (3.3 ha)	11/55	0	0	5°3′44.72″S, 38°36′18.06″E
21	24 Jul–1 Aug F (0.2B ha)	11/88	1/1 (1.1)	1/1 (1.1)	5°3′33.14″S, 38°36′02.66″E
22	24 Jul–1 Aug A (between 0.2B & 0.8 ha)	11/88	1/1 (1.1)	0	5°3′31.96″S, 38°36′02.71″E
23	24 Jul–1 Aug F (0.8 ha)	11/88	0	0	5°3′29.68″S, 38°36′02.98″E
24	24 Jul–1 Aug T	11/88	3/5 (5.7)	2/4 (4.5)	5°3′38.72″S, 38°36′18.27″E
25	24 Jul–1 Aug F (29.4 ha)	11/88	0	0	5°3′27.63″S, 38°36′24.79″E
26	26 Jul–1 Aug F (29.4 ha)	11/66	1/1 (1.5)	1/1 (1.5)	5°3′32.91″S, 38°36′20.85″E
27	26 Jul–1 Aug F (29.4 ha)	11/66	1/3 (4.5)	1/3 (4.5)	5°3′29.50″S, 38°36′22.19″E
NE portion of EU control site					
28	2–8 Aug D (control)	11/66	0	0	5°5′49.01″S, 38°36′56.49″E
29/57	2–8 Aug T	11/66	3/4 (6.1)	2/3 (4.5)	5°5′39.36″S, 38°36′57.38″E
30	2–8 Aug F (control)	11/66	1/1 (1.5)	0	5°5′38.40″S, 38°36′49.29″E
31/14, 58	2–8 Aug F (control)	11/66	4/5 (7.6)	3/3 (4.5)	5°5′37.28″S, 38°36′54.27″E
32	2–8 Aug D (control)	11/66	2/5 (7.6)	1/4 (6.1)	5°5′54.22″S, 38°37′03.17″E
33	2–8 Aug D (control)	11/66	3/5 (7.6)	2/4 (6.1)	5°6′01.47″S, 38°37′03.95″E
Bulwa					
34	8–14 Aug F (2.6 ha)	11/66	1/1 (1.5)	1/1 (1.5)	5°1′33.98″S, 38°36′57.34″E
35	9–14 Aug T	11/55	0	0	5°1′33.39″S, 38°37′02.37″E
36	9–14 Aug F (3.1 ha)	11/55	1/1 (1.8)	1/1 (1.8)	5°1′49.84″S, 38°37′23.38″E
37	9–14 Aug F (0.4 ha)	11/55	1/2 (3.6)	1/2 (3.6)	5°2′02.71″S, 38°36′51.83″E
SW portion of EU control site					
38/65	15–20 Aug F (control)	11/55	1/1 (1.8)	1/1 (1.8)	5°6′18.32″S, 38°35′54.10″E
39/66	15–25 Aug F (control)	11/110	2/2 (1.8)	2/2 (1.8)	5°6′11.49″S, 38°35′58.73″E
40/67	15–25 Aug F (control)	11/110	3/4 (3.6)	2/3 (2.7)	5°6′15.739″S, 38°36′07.67″E
41/68	15–25 Aug F (control)	11/110	3/3 (2.7)	1/1 (0.9)	5°6′22.41″S, 38°36′11.25″E
42	16–25 Aug F (control)	11/99	3/7 (7.1)	3/7 (7.1)	5°6′16.48″S, 38°35′50.25″E

TABLE 4. *Continued.*

Pitfall line/subsequent lines in same location	Dates and habitat (site)	No. of buckets/ bucket-nights	No. of species/no. of individuals (overall trap success [%])	No. of shrew species/no. of shrews (shrew trap success [%])	Coordinates
43/64	15–20 Aug T	11/55	0	0	5°6′39.52″S, 38°35′40.06″E
44/70	16–21 Aug A	11/55	1/3 (5.5)	1/3 (5.5)	5°6′38.69″S, 38°35′51.30″E
45	20–25 Aug F (control)	11/55	1/1 (1.8)	1/1 (1.8)	5°6′21.29″S, 38°35′59.91″E
46	20–25 Aug F (control)	11/55	2/2 (3.6)	2/2 (3.6)	5°6′24.51″S, 38°36′04.51″E
47	21–25 Aug F (control)	11/44	0	0	5°6′05.01″S, 38°36′03.74″E
1993					
NE portion of EU control site					
57	31 Jul–6 Aug T	11/66	1/1 (1.5)	0	5°5′39.36″S, 38°36′57.38″E
58/14, 31	31 Jul–6 Aug F (control)	11/66	1/4 (6.1)	1/4 (6.1)	5°5′37.28″S, 38°36′54.27″E
59	31 Jul–6 Aug F (control)	11/66	1/4 (6.1)	1/4 (6.1)	5°5′37.73″S, 38°36′37.98″E
60	31 Jul–6 Aug F (control)	11/66	2/5 (7.6)	2/5 (7.6)	5°5′40.48″S, 38°36′40.59″E
61	31 Jul–6 Aug F (control)	11/66	2/2 (3.0)	2/2 (3.0)	5°5′37.78″S, 38°36′32.40″E
62	1–6 Aug F (control)	11/55	2/5 (9.1)	2/5 (9.1)	5°5′42.22″S, 38°36′32.35″E
63	1–6 Aug F (control)	11/55	1/6 (10.9)	1/6 (10.9)	5°5′42.08″S, 38°36′30.96″E
SW portion of EU control site					
64/43	6–13 Aug T	11/77	2/2 (2.6)	1/1 (1.3)	5°6′39.52″S, 38°35′40.06″E
65/38	7–13 Aug F (control)	11/66	2/3 (4.5)	2/3 (4.5)	5°6′18.32″S, 38°35′54.10″E
66/39	7–13 Aug F (control)	11/66	1/3 (4.5)	1/3 (4.5)	5°6′11.49″S, 38°35′58.73″E
67/40	7–13 Aug F (control)	11/66	2/4 (6.1)	2/4 (6.1)	5°6′15.739″S, 38°36′07.67″E
68/41	7–13 Aug F (control)	11/66	2/5 (7.6)	2/5 (7.6)	5°6′22.41″S, 38°36′11.25″E
69	7–13 Aug F (control)	11/66	2/15 (22.7)	2/15 (22.7)	5°6′32.46″S, 38°36′25.25″E
70/44	7–13 Aug A	11/66	3/3 (4.5)	3/3 (4.5)	5°6′38.69″S, 38°35′51.30″E

medium-sized Sherman Traps, 23 × 9.5 × 8 cm. The Museum Specials and Victor Traps were purchased from Woodstream Corporation, Lititz, Pennsylvania; the Sherman Traps from H.B. Sherman Traps Inc., Tallahassee, Florida. These traps were set largely for rodents and placed in terrestrial or arboreal positions, along existing trails, and generally in a straight line (Fig. 8). As we sought to maximize capture success, traps were set at sites deemed likely to be frequented by small mammals, rather than at fixed distances or in a grid system. Hence, distances between consecutive traps varied. These traps were rebaited each late afternoon with freshly fried coconut coated in peanut butter. Additional details on trap techniques are given by Stanley et al. (1998). Trap lines were checked twice per day, in the early morning and mid-afternoon. A "trap-night" refers to one trap in operation for a 24 hr period (0700 to 0700 h). Table 5 lists each trap line with placement details. The term "sample-night" is used in discussion of overall sampling effort (including the number of trap-nights and bucket-nights).

Information regarding the placement of each individual trap was recorded, including trap type, measured distance from forest edge (if applicable), measured distance from consecutive traps, estimated height off the ground, details on microhabitat (i.e., under rock or horizontal on 4 cm-diameter vine), and general local habitat (Table 5). The distances between consecutive traps, often starting at the forest edge, were measured with a 50 m ribbon tape, and these distances were summed to determine the total length of each trap line.

OTHER TRAP TECHNIQUES—Tomahawk Live Traps (41 by 14 by 14 mm; Tomahawk Live Trap Co., Tomahawk, WI) were set opportunistically for squirrels, other large rodents, and small carnivores. Mist-nets (five-tiered, 12 m long, ~3 m high) were also set opportunistically for bats. Net-sets included placement over water pools and streams, bisecting trails in the forest, and at sites following the natural passage of bats. Occasionally bats were also recovered by W.D.N. from mist-nets used to survey understory birds.

Specimens

Specimens were prepared as either skins with associated skulls and axial skeletons or fixed in formalin. Standard museum measurements were taken (DeBlase & Martin, 1974): total length (from the tip of the nose to the last caudal vertebra), head and body length (from the tip of the nose to the junction of the tail and the body), tail length (from the junction of the tail and body to the last caudal vertebra), hind foot length (from the ankle to the tip of the longest claw for W.T.S., the ankle to the tip of the longest digit for S.M.G.), ear length (from the notch at the base of the ear to the longest point of the ear), and weight. Cranial measurements were taken by W.T.S. using digital calipers. Adults are defined as animals with fully erupted upper molars and the suture between the basioccipital and basisphenoid bones fused. Tissues including heart, liver, and kidney were frozen in liquid nitrogen. All voucher specimens are deposited in the Field Museum of Natural History (FMNH), Chicago, and the University of Dar es Salaam (UDSM), Dar es Salaam, Tanzania, and the tissue samples are deposited in the FMNH.

Statistical Analyses

We used a one-way ANOVA to test for differences between the external measurements of small mammals collected by

FIG. 8. Two different types of traps used to sample rodents in the forests of the East and West Usambara Mountains. Left, a Sherman Live Trap; right, a Victor Rat Trap. Note the flag hanging from the Victor Rat Trap, which was numbered for reference to individual traps. Photos by W. T. Stanley.

S.M.G. and W.T.S. There were significant differences between measurements made by these different field collectors for total length ($P \leq 0.05$), and hind foot length and ear length ($P \leq 0.001$). The differences between the datasets were not statistically significant ($P > 0.05$) for tail length, head and body length, and weight, although tail length was marginal ($P = 0.07$). These results were expected for hind foot length because W.T.S. included the claw in his measurements and S.M.G. did not. However, the differences between measurements of total length and ear length clearly indicate a difference in the way animals were manipulated and, based on these results and previous studies (Blackwell et al., 2006), we present and analyze separately the external measurements recorded by S.M.G. and W.T.S.

Systematics

We follow the taxonomy presented for shrews by Hutterer (2005); rodents by Holden (2005), Musser and Carleton (2005), Thorington and Hoffman (2005), and Woods and Kilpatrick (2005); elephant shrews by Schlitter (2005); and bats by Hoofer and Van Den Bussche (2003), Miller-Butterworth et al. (2007), Simmons (2005), and Thorn et al. (2007). FMNH catalogue numbers are presented for voucher specimens.

Results

Between 1991 and 1993, 1311 mammals were collected in the East and West Usambara Mountains. These specimens represent 12 species of crocidurine shrew, one macroscelidid elephant shrew (see Stanley et al., this volume), 19 species of bat (see Stanley & Goodman, this volume a), and 14 species of rodent (see Stanley & Goodman, this volume b). When categorized by massif, the East Usambara yielded 11 species of shrew, 17 bats, 13 rodents, and one elephant shrew and the West Usambara, seven species of shrew, 12 bats, 12 rodents, and one elephant shrew.

Most of the small mammal specimens were captured using pitfall and trap devices. A total of 18,563 sample-nights was accrued over the three years of the study, including 11,339 sample-nights (3314 bucket-nights and 8025 trap-nights) in the

TABLE 5. Summary of trap lines installed at different sites in the East and West Usambara Mountains between 1991 and 1993. Trap lines are listed by the name used in the field together with any lines set in the same general trap line location (but not in the same exact trap locations) in other years. Also presented are the dates each trap line was in place and habitat type (F = forest, D = disturbed forest, A = agricultural land, T = tea). Overall trap success includes both rodent and shrew captures. Height of traps set above ground (m) is presented as mean ± SD (range), number of traps, and percentage of total line represented by traps set off the ground. Trap line name is given to aid researchers in interpreting field notes recorded by S.M.G. and W.T.S.

Trap line/subsequent lines in same location	Dates	Habitat	No. of traps/ trap-nights	No. of species/no. of individuals (overall trap success[%])	No. of rodent species/no. of rodents (rodent trap success[%])	Length of trap line (m)	Mean distance between traps (m) ± SD (range)	Traps set above ground			Name of trap line in field notes of S.M.G. and W.T.S.	Coordinates
								Average height (m) ± SD (range)	n	% of total traps		
West Usambara												
1991												
A/AK	1–10 Jul	F	100/750	5/28 (3.7)	4/26 (3.5)						WU Site 1	5°4′3.45″S, 38°24′42.15″E
B/AL, AR	8–16 Jul	F	100/700	5/63 (9.0)	4/62 (8.9)	535	5.6 ± 4.29 (0.5–26)	1.2 ± 0.74 (0.3–3)	39	39	WU Site 2	5°4′0.45″S, 38°24′37.71″E
C	17–24 Jul	F	100/650	6/37 (5.7)	5/35 (5.4)	586	6.3 ± 8.50 (0.5–63.5)	1.0 ± 0.70 (0.1–2.5)	35	35	40 ha line	5°3′40.1″S, 38°23′ 1.63″E
D	26–31 Jul	F	31/186	4/12 (6.5)	3/11 (5.9)	87	3.2 ± 3.54 (0.3–18)	1.4 ± 0.69 (0.3–2.5)	14	45	0.8 ha line	5°4′3.54″S, 38°25′49.28″E
E	26–31 Jul	F	29/174	4/5 (2.9)	3/4 (2.3)	98	3.5 ± 3.11 (0.5–12)	1.1 ± 0.57 (0.5–2)	11	38	1.8 ha line	5°3′57.59″S, 38°26′2.73″E
F	25–31 Jul	F	50/350	5/9 (2.6)	5/9 (2.6)	—	—	1.4 ± 0.72 (0.3–3)	22	11	2.4 ha line	5°4′20.41″S, 38°25′44.59″E
G	4–12 Jul	F, A, T	50/400	5/24 (6.0)	5/24 (6.0)	GRID					Grid #1 line	5°3′48.18″S, 38°24′48.95″E
H	5–17 Jul	D	20/240	7/58 (24.2)	6/57 (23.7)						2^0 line #1	5°3′57.84″S, 38°24′37.9″E
I	11–16 Jul	F, A, T	50/250	6/19 (7.6)	6/19 (7.6)						Grid site line	5°3′39.72″S, 38°24′49.55″E
J	13–17 Jul	D	20/80	6/11 (13.8)	4/9 (11.3)						Malte's line	5°3′44.52″S, 38°24′46.15″E
K	19–24 Jul	D	40/200	2/13 (6.5)	2/13 (6.5)						*Maesopsis* line	5°3′37.34″S, 38°23′9.49″E
L	25–31 Jul	A	25/175	2/3 (1.7)	1/2 (1.1)						*Eucalyptus* line	5°4′28.03″S, 38°25′46.83″E
1992												
AK/A	28 Aug–3 Sep	F	90/450	5/58 (12.9)	5/58 (12.9)	548	6.4 ± 6.54 (0.1–36)	1.5 ± 0.74 (0.3–3)	24	27	SMG Control	5°4′3.45″S, 38°24′42.15″E
AL/B, AR	28 Aug–2 Sep	F	91/455[1]	3/52 (11.4)	3/52 (11.4)	322.5	4.8 ± 2.85 (0.3–12.6)	1.4 ± 0.50 (0.35–2.5)	26	37	WTS Control[1]	5°4′0.45″S, 38°24′37.71″E
1993												
AR/B, AL	19–23 Aug	F	60/240	5/29 (12.1)	5/29 (12.1)	325	5.5 ± 3.64 (0.5–15.5)	1.4 ± 0.38 (1–2.5)	22	37	WU Control 1993	5°4′0.45″S, 38°24′37.71″E
East Usambara												
1991												
NE portion of EU control site												
M/X, AM	5–10 Aug	F	50/250	3/11 (4.4)	3/11 (4.4)	199	4.3 ± 3.27 (0.5–13)	1.1 ± 0.68 (0.3–2.5)	18	9	Monga line 1991	5°5′36.49″S, 38°36′52.36″E
N	6–10 Aug	F, D	40/160	3/7 (4.4)	3/7 (4.4)	—	—	1.3 ± 0.53 (0.5–2)	16	40	Ecotone line	5°5′29.68″S, 38°36′56.38″E

TABLE 5. *Continued.*

Trap line/subsequent lines in same location	Dates	Habitat	No. of traps/ trap-nights	No. of species/no. of individuals (overall trap success[%])	No. of rodent species/no. of rodents (rodent trap success[%])	Length of trap line (m)	Mean distance between traps (m) ± SD (range)	Traps set above ground			Name of trap line in field notes of S.M.G. and W.T.S.	Coordinates
								Average height (m) ± SD (range)	n	% of total traps		
1992												
Monga												
O	19–24 Jul	F	30/150	3/9 (6.0)	3/9 (6.0)	40	2.3 ± 2.07 (0.5–10)	1.4 ± 0.55 (0.5–2.5)	10	33	0.1 ha line	5°3′33.78″S, 38°36′12.7″E
P	20–25 Jul	F	47/235	2/9 (3.8)	2/9 (3.8)	—	—	1.4 ± 0.85 (0.5–4)	16	34	9.4 ha A	5°3′47.69″S, 38°36′14.38″E
Q	20–25 Jul	F	45/225	2/9 (4.0)	2/9 (4.0)	—	—	1.5 ± 0.79 (.25–3)	12	27	9.4 ha B	5°3′47.69″S, 38°36′14.38″E
R	19–24 Jul	F	74/370	4/19 (5.1)	3/18 (4.9)	—	—	1.2 ± 0.75 (0.15–3)	37	50	0.45 ha line	5°3′43.75″S, 38°36′10.23″E
S	25–30 Jul	F	30/150	3/8 (5.3)	3/8 (5.3)	—	—	1.3 ± 0.67 (0.2–3)	15	50	0.42 ha line	5°3′28.63″S, 38°36′3.03″E
T	24–30 Jul	F	60/300	4/22 (7.3)	4/22 (7.3)	—	—	1.3 ± 0.68 (0.1–3)	25	42	0.8 ha line	5°3′34.3″S, 38°36′3.18″E
U	25–30 Jul	F	90/450	5/21 (4.7)	4/20 (4.4)	219	3.0 ± 3.79 (0.25–19)	1.4 ± 0.95 (0.25–4)	26	29	30 ha line	5°3′25.34″S, 38°36′18.1″E
V	24–31 Jul	M	30/210	1/1 (0.5)	1/1 (0.5)						Monga Tea Line	5°3′42.65″S, 38°36′21.04″E
W	29–31 Jul	A	50/140	3/4 (2.8)	1/2 (1.4)						Reservoir line	5°3′55.32″S, 38°36′26.38″E
NE portion of EU control site												
X/M, AM	1–7 Aug	F	70/385	4/25 (6.5)	3/24 (6.2)	221	3.5 ± 3.21 (0.5–14)	1.3 ± 0.56 (0.5–2.5)	28	40	Peninsula line	5°5′35.27″S, 38°36′50.54″E
Y	1–7 Aug	D	30/180	2/19 (10.6)	2/19 (10.6)	139	5.0 ± 1.72 (1.5–8.3)	1.0 ± 0.65 (0.2–2)	14	47	*Maesopsis* A	5°5′41.19″S, 38°37′7.32″E
Z	1–7 Aug	D	60/340	3/42 (12.4)	3/42 (12.4)	358	6.2 ± 2.49 (0.5–13)	1.2 ± 0.69 (0.1–2)	16	27	*Maesopsis* B	5°5′41.19″S, 38°37′7.32″E
Bulwa												
AA	9–13 Aug	F	40/200	3/8 (4.0)	3/8 (4.0)	—	—	1.3 ± 0.49 (0.5–2.5)	15	37	1.6 ha line	5°1′45.58″S, 38°37′27.49″E
AB	9–13 Aug	F	15/75	1/3 (5.0)	1/3 (5.0)	35.8	2.6 ± 1.58 (0.8–7.5)	1.3 ± 0.54 (0.8–2)	4	27	0.38 ha line	5°2′10.82″S, 38°36′48.38″E
AC	8–13 Aug	F	30/150	2/3 (2.0)	2/3 (2.0)	119	4.0 ± 1.97 (0.5–8.2)	1.2 ± 0.65 (0.2–2.2)	13	43	2.7 ha line	5°1′37.78″S, 38°37′2.39″E
AD	9–13 Aug	T	25/125	1/4 (3.2)	1/4 (3.2)						Bulwa Tea line	5°1′38.83″S, 38°36′58.23″E
AE	9–13 Aug	T	30/150	0/0 (0)	0/0 (0)						Bulwa Road line	5°1′37.59″S, 38°36′59.63″E
SW portion EU control site												
AF/AQ	14–20 Aug	F	62/372	6/21 (5.6)	6/21 (5.6)	191	3.6 ± 3.53 (0.25–18)	1.3 ± 0.72 (0.25–2.5)	21	34	Netline A	5°6′21.43″S, 38°35′52.07″E
AG/AP	14–20 Aug	F	100/600	5/36 (6.0)	4/35 (5.8)	627	5.5 ± 2.31 (0.2–11)	1.4 ± 0.56 (0.3–2)	34	42	Netline B[1]	5°6′21.43″S, 38°35′52.07″E
AH/AP	20–26 Aug	F	100/500[1]	4/40 (8.0)	4/40 (8.0)	226	4.2 ± 3.19 (0.1–11)	1.3 ± 0.62 (0.2–2.5)	29	48	Netline B2[1]	5°6′21.43″S, 38°35′52.07″E
AI	20–25 Aug	F	62/310	2/17 (5.5)	2/17 (5.5)	—	—	1.2 ± 0.54 (0.25–2.5)	21	34	Ridge line	5°6′31.01″S, 38°36′6.52″E

TABLE 5. *Continued.*

Trap line/subsequent lines in same location	Dates	Habitat	No. of traps/ trap-nights	No. of species/no. of individuals (overall trap success[%])	No. of rodent species/no. of rodents (rodent trap success[%])	Length of trap line (m)	Mean distance between traps (m) ± SD (range)	Traps set above ground			Name of trap line in field notes of S.M.G. and W.T.S.	Coordinates
								Average height (m) ± SD (range)	n	% of total traps		
AJ	19–24 Aug	D	30/150	2/12 (8.0)	2/12 (8.0)	179	6.0 ± 3.58 (0.5–11)	1.2 ± 0.75 (0.25–2)	8	27	*Maesopsis* C	5°6′28.95″S, 38°35′53.59″E
AS	14–19 Aug	T	30/150	0/0 (0)	0/0 (0)	—	—				Kwomkoro Tea line	
1993												
NE portion of EU control site												
AM/M, X	31 Jul–5 Aug	F	50/250	2/5 (2.0)	2/5 (2.0)	159	3.4 ± 2.82 (0.5–10)	1.6 ± 0.51 (1–2.5)	17	8.5	Peninsula	5°5′35.00″S, 38°36′50.35″E
AN	31 Jul–6 Aug	F	50/250	3/20 (8.0)	3/20 (8.0)	—	—	1.0 ± 0.58 (0.15–2)	16	8	Near Peninsula	5°5′31.96″S, 38°36′48.32″E
AO	31 Jul–6 Aug	F	100/500[1]	5/20 (4.0)	3/16 (3.2)	424	8.5 ± 3.95 (1–20)	1.5 ± 0.59 (0.6–3)	18	9	Road control 1993 A[1]	5°5′49.22″S, 38°36′49.87″E
AP/AG, AH	7–14 Aug	F	50/350[1]	6/22 (6.3)	5/21 (6.0)	513	7.7 ± 5.45 (1–20.5)	1.5 ± 0.38 (1–2)	8	27	Turaco–Bill's[1]	5°6′21.43″S, 38°35′52.07″E
AQ/AF	7–14 Aug	F	50/348	4/22 (6.3)	4/22 (6.3)	216	4.5 ± 4.08 (0.5–15)	1.2 ± 0.59 (0.25–2)	18	9	Turaco–Steve's	5°6′21.43″S, 38°35′52.07″E

[1] Metrics were based on a subset of the trap line: AG, first 80 traps; AH, first 71 traps; AL, first 71 traps; AO line, first 30 traps; AP line, last 50 traps; AQ, first 30 traps.

East Usambara and 7224 (1924 bucket-nights and 5300 trap-nights) in the West Usambara. Details of trapping effort by massif, habitat, and year are presented in Tables 2 and 3.

Trap and pitfall lines alone (excluding incidental captures by hand or specimens brought to us by local residents; see below) resulted in the capture of 1132 animals, representing 11 species of crocidurine shrew and 13 species of rodent. These two trapping methodologies yielded 10 species of shrew and 12 species of rodent in the East Usambara, and six species of shrew and 10 species of rodent in the West Usambara. The vast majority of shrews captured (91.2%) were taken in pitfall buckets; only 23 of the 263 shrews collected were taken in traps or by hand. These results are consistent with other studies of small mammals in montane regions of Tanzania (Stanley et al., 1996). In most cases, shrews obtained in traps were represented more commonly in the pitfall captures. The exception is our single specimen of *Crocidura jacksoni* collected in a Museum Special. Conversely, most rodents collected (96.6%) were taken in traps, and relatively few in pitfall buckets. However, all specimens of the rodent genus *Dendromus* (n = 11) were obtained in pitfalls.

An additional 179 mammals were collected in mist-nets, traps installed by local people, or by hand. These include single individuals of a shrew (*C. elgonius* found dead on the road) and *Petrodromus* and *Rhynchocyon* elephant shrews (see Stanley et al., this volume), 161 bats representing 19 species (see Stanley & Goodman, this volume a), and 16 rodents (nine *Heliophobius argenteocinereus*, three *Paraxerus vexillarius*, three *Lophuromys aquilus*, and one *Praomys delectorum*; see Stanley & Goodman, this volume b).

Species Accumulation Curves within and between Seasons

As previously demonstrated (Stanley et al., 1996, 1998), trap and pitfall lines combined are an effective way to sample most shrews and small to medium-sized rodents of an area. However, the duration such trapping is needed to document the fauna of an area is still unresolved. Other surveys using similar techniques in other areas of tropical Africa show different patterns. For example, extensive insectivore surveys conducted on Monts Doudou in Gabon at 110 m elevation by Goodman and Hutterer (2004) and Nicolas et al. (2004) took place a few hundred meters apart. In the first study, nine species of shrews were trapped in 264 bucket-nights, and in the second study the same species were found after 8820 bucket-nights. Hence, in this case, the number of known taxa at a relatively species-rich site plateaued in eight days of trapping with 33 installed pitfall buckets (264 accrued bucket-nights).

During a two-year study, Stanley et al. (1998) found a previously unrecorded rodent species (*Graphiurus murinus*) in the Chome Forest Reserve, South Pare Mountains, in trap lines only during the last of 22 days of sampling, after 3794 accrued trap-nights. In the East Usambara Mountains, species captured for the first time late in the study included *Crocidura usambarae*, after 3160 bucket-nights and *G. kelleni*, after 7827 trap-nights. Our trapping efforts in the East Usambara, during three years of fieldwork, did not yield an extended plateau in the species accumulation curve; two species were added to the cumulative number of species recorded in this zone during the third year, after more than 10,000 sample-nights (Figs. 9 and 10). Longer survey efforts, both within a season and across years, may be necessary to document comprehensively the small mammal fauna in the montane forests of this massif.

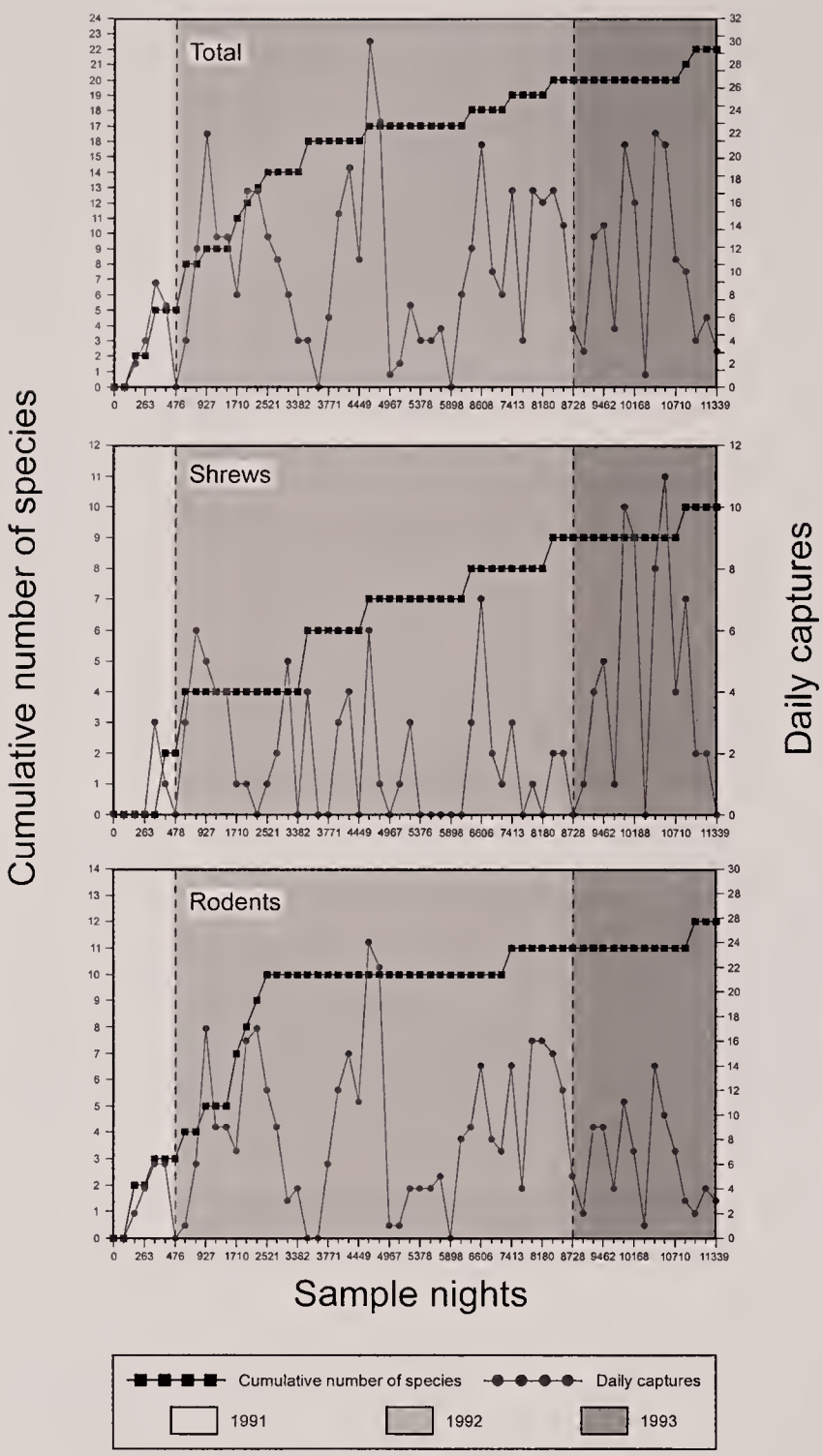


FIG. 9. East Usambara species accumulation curves showing both daily captures and cumulative number of species plotted vs. cumulative number of sample-nights. Each of the three years of the study is shaded differently.

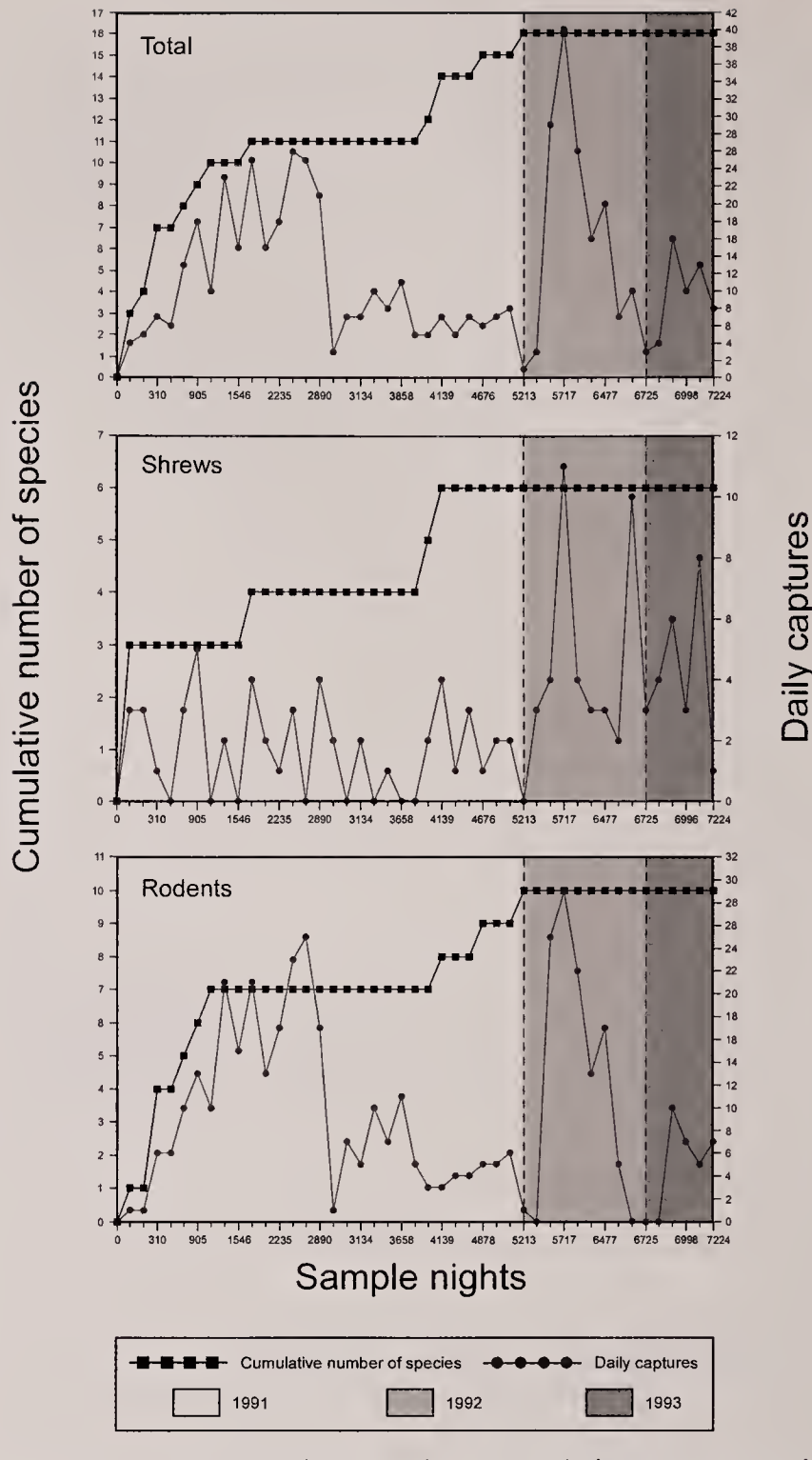


FIG. 10. West Usambara species accumulation curves showing both daily captures and cumulative number of species plotted vs. cumulative number of sample-nights. Each of the three years of the study is shaded differently.

Some of the species documented during our surveys could have been recent immigrants into the sampled habitats, either colonizing the zone naturally from lower elevations or, perhaps, even introduced by human intervention. We emphasize that patterns of species occurrence in a given forest block are not static, but dynamic. For example, based on inventory data, the resident and migratory bird fauna that the Moreaus (Moreau, 1935, 1937; Moreau & Moreau, 1937) knew in the East Usambara in the 1930s differs from that in this zone today (Stuart, 1983; Cordeiro, 1998b; Seddon et al., 1999). These aspects, overlaid on the effects of climatic change, need to be considered in future studies of the Usambara fauna.

Variation in Species Richness and Capture Rates between Seasons

Some trap and pitfall lines were placed in the same positions over two or three consecutive years of the study. In general, the pitfall buckets were placed in the same holes excavated the previous year. Although we did not place individual traps in the same exact location each consecutive year, repeated lines commenced at the same place and followed the general trail of the previous year. This replication allowed us to assess variation in abundance and diversity across the years sampled.

Figure 11 shows the results of three years of three consecutive pitfall lines (one in the East and two in the West Usambara), and two trap lines (one in each mountain range) installed in the same exact (pitfall) or general (trap) locations all three years. While abundance (based on pitfall or trap success) varied from year to year, abundance did not decrease; our removal sampling therefore did not measurably affect the abundance of shrews and rodents in the immediate area. We statistically tested this observed pattern with a one-way analysis of variance. Pitfall and trap lines in each range and year were standardized by analyzing the results of the first 11 buckets and first 35 traps of each line during the first four days the line was in operation. We found no significant difference in either the total number of individuals captured (i.e., trap success; pitfall lines: $F_{2,6} = 2.19$, $P = .19$; trap lines: $F_{2,3} = 0.16$, $P = 0.86$) or in the total number of species

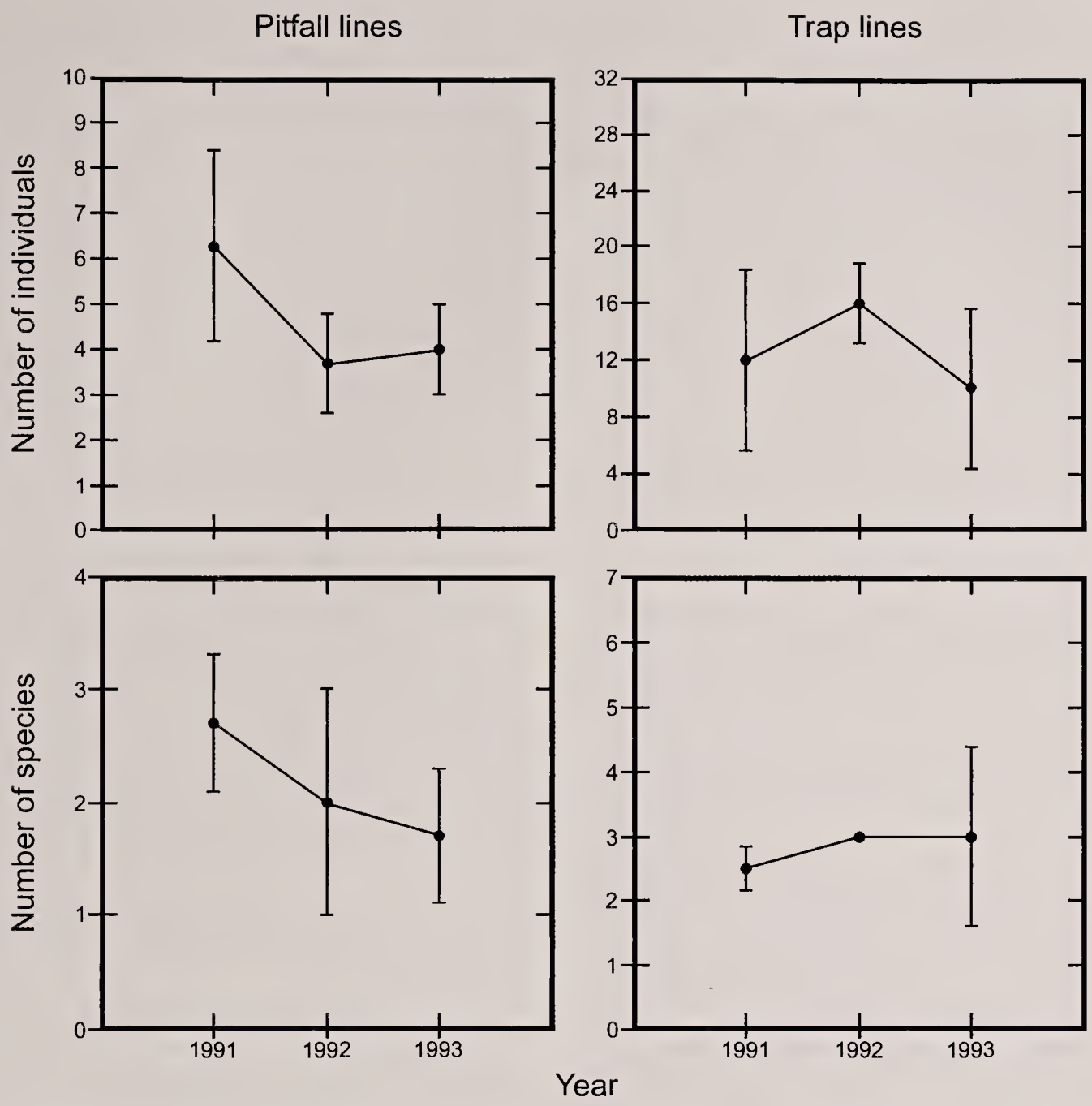


FIG. 11. Means and standard deviations of number of individuals (**top**) and species (**bottom**) captured in three pitfall lines (**left**) and two trap lines (**right**) operated over three consecutive years at the same locations in the EU and WU control sites.

captured (i.e., diversity; pitfall lines: $F_{2,6} = 1.40$, $P = 0.32$; trap lines: $F_{2,3} = 2.68$, $P = 0.21$) among the three years of the study.

Concluding Remarks

The survey data presented here and in Stanley et al. (this volume) and Stanley and Goodman (this volume a,b) highlight the mammalian diversity of the East and West Usambara Mountains. Our measures of species richness of these two massifs will almost certainly increase as new areas, at different elevations or with different habitats, are surveyed. Furthermore, on-going systematic studies using morphological and molecular genetic characters will provide insight into previously unrecognized cryptic species. These two massifs hold a rich assemblage of small mammals, with local and regional endemics, and should be the subject of continued and bolstered research and conservation activities.

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Chapter 2

Small Mammal Inventories in the East and West Usambara Mountains, Tanzania. 2. Families Soricidae (Shrews) and Macroscelididae (Elephant Shrews)

William T. Stanley[1], Steven M. Goodman[1], and Rainer Hutterer[2]

[1]*Department of Zoology, Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, IL 60605, USA*
[2]*Zoologisches Forschungmuseum Alexander Koenig, Adenauerallee 150-164, 5300 Bonn 1, Germany*

Abstract

Field surveys conducted in the montane forests of the East and West Usambara Mountains between 1991 and 1993 provide data on the species of shrews (Family Soricidae, Subfamily Crocidurinae) and elephant shrews (Family Macroscelididae). In total, 11 species of crocidurine shrew and one elephant shrew were documented on the Usambara Mountains, which include 10 shrew and one elephant shrew species for the East Usambara, and six species of shrew and one elephant shrew in the West Usambara. Information is presented on the captured animals regarding their natural history, distribution, ecology, and reproduction, as well as external and cranio-dental measurements. Species richness and different levels of endemism between the insectivorous small mammal faunas of tropical Africa and Madagascar are compared.

Introduction

The shrews (Family Soricidae, Subfamily Crocidurinae) and elephant shrews (Family Macroscelididae) of the montane areas of Tanzania are a diverse and enigmatic fauna. Recent systematic research is showing ever-increasing levels of diversity and endemism. Three of the four recognized genera within the Macroscelididae occur in Tanzania (the only genus not represented is *Macroscelides*), and the most recently described elephant shrew, *Rhynchocyon udzungwensis*, is endemic to the Udzungwa Mountains in the Eastern Arc Mountains (Schlitter, 2005; Rovero et al., 2008). Over the past century, soricids representing four genera have been described from different Tanzanian massifs, including 11 species endemic to the country, with seven having been described since 1980 (Table 1; Hutterer, 2005; Stanley et al., 2005d). The Usambara Mountains have a particularly rich shrew fauna, with at least one endemic species (*Crocidura tansaniana*; Hutterer, 2005) and one endemic subspecies (*Sylvisorex howelli usambarensis*; Hutterer, 1986).

Although some taxonomic work has been published on the shrews of the Usambaras, no thorough faunal inventory using standard protocols of pitfall trapping is yet available. This method has effectively assessed soricid diversity in other Eastern Arc Mountains, such as the Pares (Stanley et al., 1996, 2005a,b,c) and the Udzungwas (Stanley & Hutterer, 2000, 2007). Here, we report on the shrews and elephant shrews obtained during small mammal inventories in the East and West Usambara Mountains between 1991 and 1993. The principal trapping protocol used for shrews was pitfall traps, but a small percentage was captured in traps set for rodents. Information is also presented on the locally occurring elephant shrews using non-standardized field protocols.

Methodology

The trapping methodology and specifics on research sites and individual trap and pitfall lines are presented in Stanley et al. (this volume). Specimens collected were measured in the field by W.T.S. and S.M.G. External measurements (DeBlase & Martin, 1974) include total length (from the tip of the nose to the last caudal vertebra), head and body length (from the tip of the nose to the junction of the tail and the body), tail length (from the junction of the tail and body to the last caudal vertebra), hind foot length (from the ankle to the tip of the longest claw for W.T.S.; ankle to insertion of claw for S.M.G.), ear length (from the notch at the base of the ear to the longest point of the ear), and weight. All measurements were in millimeters, except weight, which was in grams. W.T.S. measured (with digital calipers to the nearest 0.01 mm) the following cranial and dental variables:

- BL (basal length): From the anterior-most aspect of the upper incisor to the anterior-most border of the foramen magnum.
- BW (bimaxillary width): The greatest breadth across the maxilla.
- CI (condylo-incisive length): From the anterior-most aspect of upper incisor to occipital condyle.
- CW (width of canine): From the most lingual to the most labial aspect of the upper canine.

TABLE 1. Soricid and macroscelidid species and subspecies endemic to different Tanzanian mountains with the site from which they were first discovered and the year of description.

Species	Type locality	Year described
Crocidura desperata	Mt. Rungwe	1991
Crocidura gracilipes	"on the way from the coast to Mt. Kilimanjaro"	1870
Crocidura monax	Mt. Kilimanjaro	1910
Crocidura tansaniana	East Usambara	1986
Crocidura telfordi	Uluguru	1986
Crocidura usambarae	West Usambara	1980
Myosorex geata	Uluguru	1927
Myosorex kihaulei	Udzungwa	2000
Myosorex zinki	Mt. Kilimanjaro	1956
Congosorex phillipsorum	Udzungwa	2005
Sylvisorex howelli	Uluguru	1984
Sylvisorex howelli usambarensis	West Usambara	1986
Rhynchocyon udzungwensis	Udzungwa	2008

- GW (greatest width of the braincase): Greatest breadth of the braincase measured at the posterior insertion of the zygomatic arches.
- HBC (height of the braincase): Measured by placing the cranium on a microscope slide, measuring from the bottom of the slide to the top of the cranium, and subtracting the thickness of the slide.
- I^3W (width of third upper incisor): From the most lingual to the most labial aspect of the third upper incisor.
- LIW (least interorbital width): Shortest distance across the cranium between the orbits.
- LTR (length of lower toothrow): From the anterior aspect of the lower incisor to the posterior aspect of the last tooth in the toothrow.
- MAST (breadth of the mastoid plate): From the posterior-most aspect of the anterior border of the mastoid plate to the anterior-most aspect of the posterior border.
- MI (length of mandible including the incisor): From the anterior aspect of the lower incisor to the posterior aspect of the articular condyle of the dentary.
- M^3L (length of third upper molar): The greatest dimension of the third upper molar.
- M^3W (width of third upper molar): The greatest dimension perpendicular to M^3L.
- NW (nasal width): The greatest breadth of the nasal bones.
- PGW (post-glenoid width): The greatest breadth across the cranium, taken just posterior to the glenoid fossa.
- PPL (post-palatal length): From the posterior border of the palate to anterior-most border of the foramen magnum.
- UTRL (length of entire upper toothrow): From the anterior-most aspect of the upper incisor to the posterior-most border of the third upper molar.

These variables follow Dippenaar (1977), van Zyll de Jong and Kirkland (1989), Carraway (1990), and Stanley and Olson (2005). Only skulls from adults (based on complete fusion between the basioccipital and basisphenoid bones) were measured. Specimens were assigned to one of four tooth wear categories, largely following the definitions of Dippenaar (1977), although we focused largely on the wear of the first upper molar. FMNH 151106, 151110, 151109, and 151117 exemplified categories I, II, III, and IV, respectively (sensu Dippenaar, 1977), and these specimens were subsequently used as a reference series for the tooth wear classification.

Standard descriptive statistics (mean, range, and standard deviation [SD]) were calculated for the different measurements of each taxon. When appropriate, we used one-way analyses of variance (ANOVA) to determine whether sexual dimorphism or geographical variation in skull dimension was significant. Although some of the sample sizes were small, and larger samples in certain cases are needed to confidently test morphological variation, we feel that comparisons of the currently available series from our field specimens are informative and generate hypotheses to be tested with additional samples and study. All statistical analyses were conducted using Systat (version 10, 2002).

Accounts of Species

Eleven species of crocidurine shrew and one elephant shrew were documented in the montane zones of the East and West Usambara Mountains after three survey seasons (see Table 2 for crocidurine shrews). For the East Usambara, 10 shrew and one elephant shrew species were confirmed, and in the West Usambara, six species of shrew were collected. External measurements for animals from both massifs are presented in Table 3. Although subsequent to the surveys reported here, W. D. Newmark found a specimen of *Rhynchocyon* in one of our study sites, and we include this record. Information regarding the natural history, including distribution, ecology and reproduction, specimens examined (including catalog numbers and pitfall lines [PF] and trap lines [TRL], from which each specimen was collected; see Stanley et al., this volume), and, when necessary, other remarks are presented for each species in the following accounts. When citing information on the testes measurements of males, the data are presented as length by width.

Family Soricidae

Subfamily Crocidurinae

Crocidura elgonius Osgood, 1910

DISTRIBUTION—First described from Mt. Elgon (Osgood, 1910), *Crocidura elgonius* is now known to occur in various montane settings in Kenya, Tanzania, and Uganda (Allen & Loveridge, 1942; Aggundey & Schlitter, 1986; Hutterer, 2005). Within Tanzania, this species has been recorded on several massifs, including Malundwe, Nguu, Udzungwa, and the East and West Usambara (Stanley et al., 1998, 2005a,b; Stanley & Hutterer, 2007; Stanley, unpubl. data). Stanley et al. (2005c) documented *C. elgonius* in Kwamgumi Forest Reserve at 300 m at the base of the East Usambara (EU). Near Amani (EU), nine of the 10 specimens collected were in non-forested habitats, eight were taken in tea plantations, and one was found in a swampy area next to a river running between the southwestern section of the EU control site and the tea plantation. The remaining animal was in relatively undisturbed forest in the northeastern section of the EU control site. In the West Usambara (WU), four specimens were trapped in disturbed habitat, including tea and *Eucalyptus*

TABLE 2. Soricomorpha species captured in three seasons of faunal surveys of the East and West Usambara Mountains between 1991 and 1993. Trap success calculated by dividing total captures by total sample-nights (see Stanley et al., this volume).

Species	East Usambara			West Usambara			Total
	1991	1992	1993	1991	1992	1993	
Crocidura elgonius	0	9	1	5	0	0	15
Crocidura fusconurina	0	1	0	0	0	0	1
Crocidura hildegardeae	2	18	24	0	0	0	44
Crocidura cf. *hirta*	0	30	0	4	0	1	35
Crocidura jacksoni	0	1	0	0	0	0	1
Crocidura cf. *mouax*	0	0	0	16	4	0	20
Crocidura olivieri	0	1	1	10	0	0	12
Crocidura tansaniana	2	12	36	0	0	0	50
Crocidura usambarae	0	0	1	0	0	0	1
Suncus megalura	0	1	2	14	3	0	20
Sylvisorex howelli	0	2	0	4	36	22	64
Total no. of individuals	4	75	65	53	43	23	263
Total no. of species	2	9	6	6	3	2	11
Accrued no. of sample-nights	476	8252	2611	5213	1512	499	18,563
Trap success for shrews (%)	0.8	0.9	2.5	1.0	2.8	4.6	1.4

plantations, and one animal was taken in forest at the 37.8-ha site.

ECOLOGY AND REPRODUCTION—In both the East and West Usambara Mountains, only this shrew was captured in tea plantations. Of 15 specimens collected from both massifs, the skulls of 10 were measured (Table 4). In the West Usambara, five specimens were collected in July 1991, which represented 9.4% of the total number of shrews taken that year. Of these, two were female, two were male, and the sex of one was not determined. One male had abdominal testes measuring 4 by 3 mm. One female had small teats, and the other was lactating. All specimens from the East Usambara (captured in the months of July and August in 1992 and 1993) were males; the average testes measurements of examined animals (n = 6) were 3.0 (range = 2–4 mm, SD = 0.6) by 1.8 mm (1–2 mm, 0.4).

REMARKS—External and cranio-dental measurements are given in Tables 3 and 4.

SPECIMENS EXAMINED—**EAST USAMBARA**, 4.5 km ESE Amani, Monga Tea Estate, EU control site (PF 70—FMNH 151052); 4.5 km WNW Amani, Monga Tea Estate, EU control site (PF 29—FMNH 149944; PF 31—FMNH 150374); 6 km NW Amani, Monga Tea Estate (PF 16—FMNH 149940–149943, 150373; PF 24—FMNH 149945, 150377); **WEST USAMBARA**, 11 km NW Korogwe, Ambangulu Tea Estate (PF 10—FMNH 147194–147196; found dead on the road—FMNH 147351); 14.5 km NW Korogwe, Ambangulu Tea Estate (PF 8—FMNH 147193).

Crocidura fuscomurina (Heuglin, 1865)

DISTRIBUTION—*Crocidura fuscomurina* was described based on a specimen collected in a swampy area at Meshra-el-Req, Sudan. This species has been reported from across much of sub-Saharan Africa. Hutterer (1983) discussed the taxonomy and distribution of this species and cautioned that many references in the literature may involve misidentifications. Hutterer (2005) identifies the known synonyms of this species, including *C. bicolor* Bocage, 1889. Laurie (1971) documented this species (as *C. bicolor*) in Serengeti National Park, and Allen and Loveridge (1942) mentioned specimens from just north of Lindi on the Tanzanian coast. Stanley et al. (2005b) documented *C. fusconurina* at 1100 m in the Udzungwa Mountains National Park, but it has rarely been recorded in other small mammal surveys in montane habitats of Tanzania (Stanley et al., 1998). However, Oguge et al. (2004) found this species in the Taita Hills (part of the Eastern Arc Mountains) and the Shimba Hills of Kenya.

Our study generated only one specimen, collected in the East Usambara in a pitfall trap on 23 August 1992 in secondary forest dominated by *Maesopsis* trees. Oliver et al. (2002) recorded a specimen, tentatively identified as *C. bicolor* from the Mgambo Forest Reserve, in the northeastern portion of East Usambara at 560 m in open woodland; we have been unable to examine the specimen to verify the species identification.

ECOLOGY AND REPRODUCTION—Information on the ecology of *C. fuscomurina* in Tanzania is limited. The single specimen captured during our study was in a pitfall line in the northeastern section of the EU control site. It was a male found dead and partially eaten by crabs, with the skull damaged. See Table 3 for external measurements. Laurie (1971) found crania and lower jaws of this species in the regurgitated pellets of the Barn Owl (*Tyto alba*) in the Serengeti National Park.

SPECIMENS EXAMINED—**EAST USAMBARA**, 4.5 km ESE Amani, Monga Tea Estate, EU control site (PF 42—FMNH 150668).

Crocidura hildegardeae Thomas, 1904

DISTRIBUTION—*Crocidura hildegardeae* has been recorded from several areas across eastern and central Africa, including mountains in northern and southern Tanzania. This species has been documented in the North and South Pare Mountains (Stanley et al., 1996, 2007a), Mt. Kilimanjaro (Stanley, unpubl. data), Mt. Meru (Demeter & Hutterer, 1986), and the Udzungwa Mountains (Stanley & Hutterer, 2007) but has not been found during intensive surveys of massifs within the central Eastern Arc Mountains, such as the Nguru, Nguu, Ukaguru, and Uluguru (Stanley et al., 1998; Stanley, unpubl. data). Intensive sampling during the fieldwork of our study found *C. hildegardeae* in the East, but not in the West Usambara, where *Sylvisorex howelli*, a shrew of similar size, was common. Oguge et al. (2004) documented *C. hildegardeae* in many forests of southeastern Kenya, including the Taita Hills.

ECOLOGY AND REPRODUCTION—Forty-four specimens of *C. hildegardeae* were collected in East Usambara over the three years of this study, including two, 18, and 24 individuals in

1991, 1992, and 1993, respectively. The species was generally found in forested habitats. The only animal captured outside of natural forest habitat was in PF 64 (see Stanley et al., this volume), placed at the ecotone between a tea plantation and herbaceous vegetation. It was captured in the same bucket as the rodent *Lophuromys aquilus* (True, 1892). All other *C. hildegardeae* specimens were collected from both disturbed and pristine forested habitats, with 37 of the 43 specimens (86%) coming from the EU control site and six (14%) from one of the fragments (0.2-ha fragment [n = 1], 3.3-ha fragment [n = 1], and 29.4-ha fragment [n = 4]).

In 1992, three females with large teats were captured, neither of the two examined were carrying embryos. All six females captured in 1993 were examined, and three (50%) were pregnant, all with two embryos, one in each uterine horn, and the crown–rump length ranged from 9 to 12 mm (mean = 10.3 mm). In 1991, one male was examined and the testes measured 5 by 4 mm. In 1992, 13 males were inspected and the mean testis measurements were 3.9 (range = 2–5 mm, SD = 0.76) by 2.7 mm (range = 1–5 mm, SD = 0.94). In 1993, 14 males were checked, and the mean testis measurements were 3.9 (range = 2–5 mm, SD = 0.84) by 2.5 mm (range = 1–4 mm, SD = 0.76).

A one-way ANOVA of the cranio-dental measurements of adults indicated males were significantly larger than females in most of the variables (Table 5). A similar pattern of sexual dimorphism was found in this species in the South Pare (Stanley et al., 1996). Hence, we present the external measurements of each sex separately in Table 3.

Specimens Examined—**EAST USAMBARA**, 4.5 km ESE Amani, Monga Tea Estate, EU control site (PF 38—149960; PF 39—FMNH 149956; PF 40—FMNH 149954, 150380; PF 41—FMNH 150385; PF 42—FMNH 149953, 149955, 150386; PF 46—FMNH 149957; PF 64—FMNH 151072; PF 65—FMNH 151053, 151075; PF 66—FMNH 151057, 151063, 151074; PF 67—FMNH 151061, 151062; PF 68—FMNH 151058, 151059, 151070, 151071; PF 69—FMNH 151060, 151069, 151073); 4.5 km WNW Amani, Monga Tea Estate, EU control site (PF 14—FMNH 147197, 147198; PF 33—149950–149952; PF 59—FMNH 151054, 151056, 151067, 151068; PF 60—FMNH 151055, 151065, 151066, 151368; PF 61—FMNH 151064); 6 km NW Amani, Monga Tea Estate (PF 18—FMNH 149947; PF 19—FMNH 149946; PF 26—FMNH 148949; PF 27—FMNH 149948, 149958, 149959).

Crocidura hirta Peters, 1852

Distribution—We tentatively identify the samples listed here as *Crocidura hirta*, although another possible name to apply to the Usambara animals is *C. xantippe* Osgood, 1910, which has also been noted as occurring in the Usambara Mountains (Heim de Balsac & Meester, 1977; Hutterer, 2005). Hutterer (2005) indicated that *C. xantippe* is probably related to *C. hirta*; this is a question that can only be resolved with a series of voucher specimens across a broad geographic range. We have identified specimens as *C. hirta* from sites in other areas of Tanzania (Stanley et al., 1996, 2000, 2005a,b,c, 2007a,b,c). A taxonomic revision of *C. hirta* is needed.

Ecology and Reproduction—Thirty-five specimens referred to *C. hirta* were collected during our study, including 30 from the East and five from the West Usambara Mountains. Most were captured in small forest fragments, in agricultural areas or tea plantations. Only two individuals (6%) were collected in forested areas, in this case, as singletons in the control areas of the East and West Usambara Mountains. Of the remainder, only one (3% of total) was captured in the 29.4-ha East Usambara fragment. In the West Usambara, one and two individuals were trapped in the 0.8- and 1.9-ha fragment, respectively, and one was collected in a *Eucalyptus* plantation. In the East Usambara sites, nine animals were obtained in a tea plantation, three in an agricultural area, and the remainder (16) in forest fragments (all <10 ha in size).

Of the total collected, 34 skulls were aged following Dippenaar (1977); 12 (35%) were juvenile and excluded from analysis of cranio-dental measurements. One skull, the smallest (FMNH 149982), is listed separately in Table 6 and was not included in subsequent analyses. This specimen was captured in the 0.2-ha fragment and is tentatively identified as *C. hirta*. A one-way ANOVA was conducted with the East Usambara sample (the largest) to test for sexual dimorphism in cranial measurements (three females and 13 males), and no significant difference was found. We then combined sexes to test for differences between the samples from the two different mountains, and no significant variation was observed. The descriptive statistics for each external and cranio-dental character measured are given for all samples combined in Tables 3 and 6.

Specimens Examined—**EAST USAMBARA**, 4.5 km ESE Amani, Monga Tea Estate, EU control site (PF 44—FMNH 149997, 149998, 150006); 4.5 km WNW Amani, Monga Tea Estate, EU control site (PF 29—FMNH 149984, 150005; PF 31—FMNH 149995); 6 km NW Amani, Monga Tea Estate (PF 16—FMNH 149981, 149988, 150002–150004; PF 17—FMNH 149963, 149964, 149983, 149991, 149992; PF 18—FMNH 149982; PF 19—FMNH 149962, 149966, 149967, 149990; PF 21—FMNH 149965; PF 24—FMNH 149993, 149994; TRL R—FMNH 149989; TRL U—FMNH 149986); 8 km NWN Amani, Bulwa Tea Estate (PF 34—FMNH 150378; PF 36—FMNH 149985; PF 37—FMNH 149987, 149996); **WEST USAMBARA**, 11 km NW Korogwe, Ambangulu Tea Estate (PF 12—FMNH 147359; PF 13—FMNH 147212, 147214; TRL L—FMNH 147213); 12.5 km NW Korogwe, Ambangulu Tea Estate (PF 73—FMNH 151099).

Crocidura jacksoni Thomas, 1904

Distribution—Oguge et al. (2008) include the eastern section of the Democratic Republic of the Congo, Uganda, Kenya, and northern Tanzania in the known distribution of *Crocidura jacksoni*. In Kenya, this species has been documented in the Taita Hills (the northern-most range of the Eastern Arc Mountains), including Mt. Sagala and Mt. Kasigau from elevations ranging from 1300 to 2200 m (Oguge et al., 2004). Similar trapping efforts during the study of Oguge and colleagues did not capture *C. jacksoni* in the volcanic Kyulu Hills, roughly 80 km to the northwest of the Taita Hills. Aggundey and Schlitter (1986) listed a variety of localities across Kenya with voucher specimens of this taxon. Within Tanzania, documented occurrences are few but include specimens from the Tarangire National Park (Stanley et al., 2007c).

Within the Usambara forests, Cunneyworth et al. (1997) report the capture of *C. jacksoni* at the southern edge of Kambai Forest Reserve, a lowland site (about 600 m) with grassy understory. However, no indication was given about the collection of a voucher specimen, which is needed to verify this record.

Ecology and Reproduction—One female specimen was collected on 30 July 1992 in a clump of bamboo in a marshy

TABLE 3. External measurements (mm) and weight (g) of adult shrew and elephant shrew species collected during the 1991–1993 surveys of the East (EU) and West Usambara (WU) Mountains, including total length (TL), head and body length (HB), length of tail vertebrae (TV), hind foot length (HF), ear length (EAR), and weight (WT). Measurements taken by S.M.G. are presented separately from those of W.T.S. (see Stanley et al., this volume). Within these subsets, measurements were subjected to a one-way ANOVA to test for effect of sex or locality (mountain range). If not significant, the samples were pooled to derive the summary statistics. Descriptive statistics are presented as mean ± standard deviation, range, and (sample size).

Species	TL	HB	TV	HF	EAR	WT
Crocidura elgonius EU and WU						
S.M.G.						
Mean ± SD	99.0 ± 5.55	55.8 ± 2.50	39.9 ± 3.48	9.4 ± 0.52	7.1 ± 0.83	3.4 ± 0.41
Range	91–107	53–59	35–45	9–10	6–8	2.5–3.8
n	8	4	8	8	8	8
W.T.S.						
Mean ± SD	92.0 ± 4.64	55.4 ± 3.29	36.2 ± 1.79	10.0 ± 0.71	7.6 ± 0.55	3.3 ± 0.50
Range	86–99	51–59	33–38	9–11	7–8	2.8–4.1
n	5	5	5	5	5	5
Crocidura fuscomurina EU						
S.M.G.	119	73	45	12	—	5.1
Crocidura hildegardeae EU						
S.M.G. females	122	76	49	12	9	5.9
S.M.G. males						
Mean ± SD	123.2 ± 5.04	73.2 ± 5.09	49.3 ± 2.89	12.8 ± 1.77	9.2 ± 0.65	6.8 ± 0.93
Range	109–129	63–81	44–54	8–17	8–10	5.5–8.8
n	18	15	18	18	18	18
W.T.S. Females						
Mean ± SD	116.1 ± 4.85	69.9 ± 5.96	44.4 ± 1.81	12.3 ± 0.46	8.5 ± 0.53	6.1 ± 0.92
Range	108–123	60–77	43–47	12–13	8–19	4.3–7
n	7	8	7	8	8	8
W.T.S. Males						
Mean ± SD	118.2 ± 5.66	71.9 ± 5.23	46.4 ± 3.20	13.1 ± 0.75	8.8 ± 0.66	6.7 ± 1.20
Range	105–126	60–78	37–51	12–14	8–10	4.8–8.7
n	17	17	17	17	17	17
Crocidura hirta EU and WU						
S.M.G.						
Mean ± SD	151.6 ± 13.71	82.1 ± 8.57	62.9 ± 5.29	15.1 ± 1.35	10.4 ± 1.11	10.8 ± 3.11
Range	125–176	66–95	55–72	12–18	8–12	6.1–14.5
n	14	10	14	14	14	14
W.T.S.						
Mean ± SD	147.5 ± 10.00	86.1 ± 6.54	60.9 ± 4.13	15.5 ± 0.98	10.0 ± 0.80	10.9 ± 2.79
Range	127–163	75–98	50–67	14–17	9–11	5.9–14.5
n	20	20	20	20	14	21
Crocidura jacksoni EU						
S.M.G.	147	85	65	15	5	8
Crocidura monax WU						
S.M.G.						
Mean ± SD	159.8 ± 5.84	–	65.7 ± 3.07	16.2 ± 0.73	10.4 ± 0.65	13.9 ± 1.55
Range	150–170		60–71	15–17	9.5–12	10–16.5
n	16		18	18	17	17
W.T.S.						
Mean ± SD	158.5 ± 2.12	–	64.5 ± 2.12	17.0 ± 0.00	10.0 ± 0.00	12.3 ± 0.35
Range	157–160		63–66	17–17	10–10	12–12.5
n	2		2	2	2	2
Crocidura olivieri EU and WU						
S.M.G.						
Mean ± SD	210.9 ± 9.47	113	88.8 ± 4.97	21.1 ± 1.24	11.6 ± 0.92	32.1 ± 7.56
Range	195–224		80–98	19–23	10–13	23.5–45
n	12		12	12	11	12
Crocidura tansaniana						
S.M.G.						
Mean ± SD	167.2 ± 8.52	98.7 ± 5.62	68.8 ± 4.53	16.3 ± 0.74	12.0 ± 1.33	14.6 ± 2.09
Range	151–184	87–110	60–76	15–18	8–14	9.5–20
n	26	18	26	26	26	26
W.T.S.						
Mean ± SD	160.4 ± 11.26	93.5 ± 8.32	67.6 ± 4.70	17.2 ± 0.87	10.7 ± 0.79	14.6 ± 3.02
Range	130–176	73–105	54–75	15–19	9–12	6.6–20
n	25	25	25	25	25	25

TABLE 3. *Continued.*

Species	TL	HB	TV	HF	EAR	WT
Crocidura usambarae EU						
W.T.S. EU	145	84	61	15	10	8.5
Suncus megalura EU & WU						
S.M.G.						
Mean ± SD	165.7 ± 5.46	69.5 ± 3.54	91.7 ± 4.08	15.8 ± 0.66	10.3 ± 1.60	6.2 ± 0.57
Range	157–181	67–72	81–101	15–17	9–16	5–7.5
n	16	2	16	16	16	16
W.T.S.						
Mean ± SD	161.0 ± 4.32	70.8 ± 2.75	92.0 ± 2.16	16.0 ± 0.00	9.5 ± 0.58	6.0 ± 0.97
Range	157–167	68–74	89–94	16–16	9–10	5.2–7.4
n	4	4	4	4	4	4
Sylvisorex howelli EU						
S.M.G.	103	61	45	11	8	3.3
W.T.S.	98	52	41	10	8	3.5
Sylvisorex howelli WU						
S.M.G.						
Mean ± SD	106.2 ± 3.61	65.1 ± 2.56	43.4 ± 2.23	11.1 ± 0.54	8.5 ± 0.65	3.9 ± 0.52
Range	100–112	61–72	39–48	10–13	7.5–10	2.5–5
n	21	21	21	22	22	21
W.T.S.						
Mean ± SD	101.8 ± 5.10	60.6 ± 4.41	40.7 ± 2.17	11.0 ± 0.54	8.3 ± 0.71	3.8 ± 0.36
Range	91–111	52–68	36–46	9–12	8–12	2.9–4.6
n	42	42	42	42	42	42
Petrodromus tetradactylus EU						
S.M.G.	380	—	175	56	37	197

area next to a man-made pond below the Monga Tea Estate factory. The specimen was partially consumed by ants, with damage to the ears (Table 3).

REMARKS—Oguge et al. (2008) mentioned that the species is relatively common and widespread in some portions of its range, without referring to specific localities. Our trapping results in the montane forests of the Usambara Mountains indicate that it is notably uncommon, with the only record being from the East Usambara.

SPECIMENS EXAMINED—**EAST USAMBARA**, 6 km NW Amani, Monga Tea Estate (TRL W—FMNH 150606).

Crocidura monax Thomas, 1910

DISTRIBUTION—*Crocidura monax* was described from specimens collected on Mt. Kilimanjaro, to the northwest of the Usambara Mountains, and few details are known concerning its geographical range. Burgess et al. (2000) considered this taxon to be restricted to Mt. Kilimanjaro. We trapped this species only on the West Usambara. Conversely, we collected a similarly sized species, *C. tansaniana*, only on the East Usambara. Stanley et al. (1998) tentatively identified medium-sized shrews (10–17 g) obtained during surveys of other

TABLE 4. Cranio-dental measurements of *Crocidura elgonius* from the East and West Usambara Mountains with results of a one-way ANOVA to test for significant differences between mountains.

	East Usambara (n = 6)		West Usambara (n = 4)			
Measurement	Mean ± SD	Range	Mean ± SD	Range	F	P
CI	16.1 ± 0.31	15.6–16.5	15.9 ± 0.12	15.8–16.0	1.21	0.30
BL	14.4 ± 0.32	13.9–14.8	14.2 ± 0.09	14.2–14.3	0.68	0.43
PPL	7.3 ± 0.19	7.1–7.6	7.3 ± 0.05	7.2–7.3	0.38	0.55
UTR	6.8 ± 0.16	6.5–6.9	6.7 ± 0.02	6.6–6.7	1.55	0.24
LIW	3.3 ± 0.09	3.2–3.4	3.4 ± 0.08	3.3–3.5	0.34	0.58
BW	4.7 ± 0.12	4.6–4.9	4.7 ± 0.08	4.6–4.8	0.06	0.82
NW	1.4 ± 0.07	1.3–1.5	1.4 ± 0.09	1.2–1.4	0.91	0.37
GW	7.1 ± 0.13	6.9–7.3	7.1 ± 0.14	6.9–7.3	0.24	0.64
HBC	4.6 ± 0.43	4.1–5.3	4.4 ± 0.20	4.3–4.7	0.40	0.54
I3W	0.5 ± 0.02	0.5–0.5	0.5 ± 0.02	0.4–0.5	4.56	0.06
CW	0.5 ± 0.02	0.5–0.5	0.5 ± 0.03	0.5–0.5	0.47	0.51
M3L	0.9 ± 0.05	0.9–1.0	0.9 ± 0.06	0.8–1.0	0.70	0.42
M3W	0.4 ± 0.04	0.4–0.5	0.4 ± 0.03	0.4–0.4	2.02	0.19
Mast	0.6 ± 0.06	0.5–0.7	0.7 ± 0.05	0.7–0.8	4.23	0.07
MI	9.4 ± 0.23	9.0–9.6	9.3 ± 0.14	9.2–9.5	0.57	0.47
LTR	6.3 ± 0.14	6.1–6.4	6.2 ± 0.03	6.1–6.2	1.15	0.32

TABLE 5. Cranio-dental measurements of male and female *Crocidura hildegardeae* from the East Usambara with results of a one-way ANOVA to test for significant differences between sexes.

	Females (n = 6)		Males (n = 25)		
Measurement	Mean ± SD	Range	Mean ± SD	Range	F
CI	18.5 ± 0.29	18.0–18.8	19.2 ± 0.36	18.1–19.6	22.8***
BL	16.7 ± 0.23	16.4–17.1	17.3 ± 0.31	16.4–17.8	19.9***
PPL	8.4 ± 0.17	8.2–8.7	8.7 ± 0.19	8.2–9.0	12.4**
UTR	7.9 ± 0.13	7.8–8.1	8.2 ± 0.13	7.9–8.4	22.7***
LIW	3.9 ± 0.03	3.9–3.9	4.0 ± 0.11	3.8–4.2	2.8
BW	5.7 ± 0.08	5.6–5.8	5.8 ± 0.13	5.5–6.1	4.5*
NW	1.5 ± 0.06	1.4–1.6	1.6 ± 0.06	1.4–1.7	1.5
GW	8.6 ± 0.15	8.4–8.7	8.8 ± 0.15	8.4–9.1	9.7**
HBC	5.5 ± 0.19	5.3–5.8	5.6 ± 0.16	5.2–5.9	1.2
I3W	0.6 ± 0.02	0.5–0.6	0.6 ± 0.02	0.5–0.6	5.8*
CW	0.6 ± 0.02	0.6–0.6	0.6 ± 0.02	0.6–0.7	4.1
M3L	1.2 ± 0.02	1.2–1.2	1.2 ± 0.04	1.2–1.3	0.9
M3W	0.6 ± 0.02	0.5–0.6	0.6 ± 0.03	0.6–0.7	5.2*
Mast	0.9 ± 0.08	0.9–0.6	1.0 ± 0.11	0.7–1.2	0.3
MI	11.2 ± 0.10	11.0–11.3	11.6 ± 0.22	11.0–12.0	21.4***
LTR	7.3 ± 0.13	7.1–7.5	7.5 ± 0.12	7.3–7.7	17.3***

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

montane habitats in Tanzania as *C. monax*, pending a thorough analysis of this material with specimens from the type locality.

ECOLOGY AND REPRODUCTION—Sixteen specimens were collected in 1991 (12 males and four females) and four males in 1992. One female was examined for reproductive activity and was nulliparous. From the 1991 and 1992 collections, the reproductive condition of four males was examined each year. In 1991, the average testis measurement was 4.2 mm (range = 4–5 mm) by 3.0 mm (2–4 mm) and in 1992, 5.2 mm (3–6 mm) by 3.0 mm (2–4 mm). All the specimens, except two, came from the WU control site and the balance from the 37.8-ha and 1.5-ha fragments of that massif.

REMARKS—A one-way ANOVA found no significant difference between sexes in cranio-dental measurements. Hence, the sexes were pooled to compare cranio-dental differences between specimens from the West Usambara and those recently collected from Mt. Kilimanjaro. In all but three measurements (post-palatal length, least interorbital width, and height of the braincase), the West Usambara sample was significantly larger than that from Mt. Kilimanjaro (Table 7). The taxonomic implications of these differences are under study, including samples of "*monax*" from other mountains in Tanzania (see Remarks under *C. tansaniana*).

SPECIMENS EXAMINED—**WEST USAMBARA**, 12.5 km NW Korogwe, Ambangulu Tea Estate (PF 1—FMNH 147205, 147206, 147352; PF 2—FMNH 147354; PF 5—FMNH 147204, 147207–147209, 147356–147358; PF 48—FMNH 149979, 149980; PF 49—FMNH 149999; PF 53—FMNH 150000; TRL B—FMNH 147355; TRL H—FMNH 147353; TRL J—FMNH 147203, 147376); 14.5 km NW Korogwe, Ambangulu Tea Estate (PF 7—FMNH 147210).

Crocidura olivieri (Lesson, 1827)

DISTRIBUTION—*Crocidura olivieri* is distributed from Egypt to South Africa, and this large-bodied shrew (average weight 35 g) is found in various habitats across its range. Within eastern Africa, *C. olivieri* has been reported from numerous sites, including the Taita Hills, Mt. Kilimanjaro, and the South Pare, North Pare, Nguru, Nguu, Uluguru, Ukaguru, Udzungwa, Rungwe, and Mahale Mountains (Stanley et al., 1996, 1998, 2007b; Oguge et al., 2004; Stanley & Hutterer, 2007). Cunneyworth et al. (1997) captured this species in Kambai Forest Reserve, between 500 and 800 m, on the East Usambara.

ECOLOGY AND REPRODUCTION—We collected 12 specimens of *C. olivieri* in the Usambaras, with 10 (83%) at West Usambara sites—six were taken in the WU control and two in the 37.8-ha and one each in the 1.9-ha and 1.5-ha fragments. The two specimens from the East Usambara were taken in the EU control site. Singleton females from each mountain were examined for reproductive condition; neither was pregnant. One male collected 5 August 1992 had testes that measured 6 by 4 mm with convoluted epididymides. Three males from the

TABLE 6. Cranio-dental measurements of *Crocidura hirta* from the East and West Usambara Mountains. FMNH 149982 is listed separately (see text).

	C. hirta (n = 21)		
Measurement	Mean ± SD	Range	FMNH 149982
CI	22.8 ± 0.46	21.7–23.9	20.4
BL	20.6 ± 0.44	19.6–21.6	18.8
PPL	10.0 ± 0.27	9.5–10.5	9.5
UTRL	9.9 ± 0.23	9.3–10.5	8.9
LIW	4.7 ± 0.15	4.4–5.0	4.4
BW	7.0 ± 1.80	6.7–7.3	6.6
NW	1.9 ± 0.12	1.7–2.2	1.9
GW	9.8 ± 0.28	9.4–10.7	9.2
PMH	6.2 ± 0.21	5.9–6.7	5.7
PGW	6.8 ± 0.19	6.6–7.2	6.2
M&I	13.9 ± 0.37	13.2–14.9	12.6
LTR	9.1 ± 0.23	8.6–9.7	8.3
I3W	0.80 ± 0.06	0.7–1.0	0.7
CW	0.80 ± 0.06	0.7–1.0	0.7
M3L	1.5 ± 0.09	1.4–1.7	1.4
M3W	0.7 ± 0.05	0.6–0.9	0.6
MAST	1.1 ± 0.12	0.9–1.4	0.8

TABLE 7. Comparison of cranio-dental measurements between samples of *Crocidura monax* from Mt. Kilimanjaro and the West Usambara, with results of a one-way ANOVA to test for significant differences between localities.

	Mt. Kilimanjaro (n = 54)		West Usambara (n = 18)		
	Mean ± SD	Range	Mean ± SD	Range	F
CI	23.2 ± 0.48	22.3–24.1	23.7 ± 0.46	22.9–24.7	11.084**
BL	21.0 ± 0.43	20.3–21.9	21.4 ± 0.44	20.8–22.4	8.844**
PPL	10.6 ± 0.24	10.0–11.1	10.6 ± 0.28	10.0–11.1	1.101
UTRL	10.2 ± 0.20	9.7–10.6	10.5 ± 0.23	10.0–11.0	20.458***
LIW	5.2 ± 0.14	4.8–5.5	5.1 ± 0.19	4.6–5.4	0.590
BW	7.1 ± 0.13	6.8–7.3	7.3 ± 0.16	7.1–7.6	59.597***
NW	1.9 ± 0.10	1.6–2.1	2.1 ± 0.11	1.8–2.3	51.505***
GW	10.4 ± 0.25	9.9–11.0	10.6 ± 0.29	10.0–11.0	6.109*
PMH	7.0 ± 0.32	6.4–8.0	6.9 ± 0.25	6.3–7.4	1.434
M&I	14.8 ± 0.35	14.0–15.5	15.0 ± 0.42	14.0–15.7	5.178*
LTR	9.5 ± 0.18	9.0–9.8	9.7 ± 0.24	9.1–10.3	13.907***
I3W	0.80 ± 0.03	0.71–0.87	0.96 ± 0.05	0.80–1.02	243.089***
CW	0.90 ± 0.04	0.80–0.97	1.00 ± 0.06	0.80–1.05	65.281***
M3L	1.57 ± 0.06	1.44–1.69	1.71 ± 0.06	1.59–1.79	72.453***
M3W	0.84 ± 0.04	0.74–0.95	0.87 ± 0.06	0.75–0.98	6.547*
MAST	1.00 ± 0.11	0.75–1.31	1.19 ± 0.09	1.06–1.40	40.712***

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

West Usambara sites (all collected in July) were examined: the testes ranged from 2 to 6 by 3 to 4 mm, and only one had convoluted epididymides. See Table 3 for external measurements.

No significant morphological variation was found between samples from the East and West Usambara Mountains. This species is the largest shrew in Tanzania and one of the largest in Africa. Although we have no direct evidence, we strongly suspect that it is able, on occasion, to climb out of our 15-liter pit-fall buckets. Hence, we do not include this species in comparisons of pitfall results among forest fragments.

SPECIMENS EXAMINED—**EAST USAMBARA**. 4.5 km WNW Amani, Monga Tea Estate, EU control site (TRL X—FMNH 149968; TRL AO—FMNH 151101). **WEST USAMBARA**. 12.5 km NW Korogwe, Ambangulu Tea Estate (PF 1—FMNH 147199; PF 3—FMNH 147361; PF 5—FMNH 147362, 147363; TRL A—FMNH 147200, 147201); 14.5 km NW Korogwe, Ambangulu Tea Estate (TRL C—FMNH 147364, 147365); 11 km NW Korogwe, Ambangulu Tea Estate (TRL D—FMNH 147202; TRL E—FMNH 147366).

Crocidura tansaniana Hutterer, 1986

DISTRIBUTION—*Crocidura tansaniana* was described based on a specimen collected near Amani, East Usambara (Hutterer, 1986). This species was quite common in the forests we sampled in the East Usambara, but, during our study, it was not documented in the West Usambara. *Crocidura monax*, which is similar in size (10–20 g) to *C. tansaniana*, was common in the West Usambara forests (see under that taxon).

ECOLOGY AND REPRODUCTION—Between 1991 and 1993, 50 specimens were collected comprising 20 females and 30 males, including two males in 1991, three females and nine males in 1992, and 17 females and 18 males in 1993. The higher number of captures of this species in 1993 may reflect more extensive sampling effort in the northeastern and southwestern portions of the EU control site, where most specimens were collected. The only exception was an animal obtained in the 3.3-ha fragment near Monga. Of 102 shrews trapped between 1991 and 1993 at the EU control site, 48 were *C. tansaniana* (47%). There were yearly fluctuations in the number of *C. tansaniana* captured relative to other shrew species—in 1991, four of eight shrews obtained were *C. tansaniana*, and the other half were *C. hildegardeae*; in 1992, *C. tansaniana* made up 35% of the shrews captured (12/34); and in 1993, *C. tansaniana* constituted 55% of the shrews trapped (35/64). In 1993, 12 of the 35 *C. tansaniana* specimens (34%) came from one pitfall line (PF 69). This line was installed in primary forest in the southeastern portion of the EU control site and was positioned across a valley where the soil was very fine and clay-like.

Of the 18 males examined over the three-year study for reproductive condition, the average testis measurements were 4.4 mm (range = 3–6 mm) by 2.4 mm (1.5–4 mm). Measurements of examined males for each year include: 1991, one with testes 6 by 4 mm; 1992, seven males with mean measurements of 4.3 by 2.1 mm; and 1993, nine males with mean measurements of 4.6 by 2.6 mm. In 1992, two females were examined: one was pregnant with a single embryo in each uterine horn and the largest embryo measuring 14 mm in crown–rump length. In 1993, 11 females were dissected, and only a single animal was pregnant, with one embryo in each uterine horn and the largest embryo measuring 8 mm in crown–rump length. Over the two years, 17 females were examined for teat condition—eight were noted as small, seven large, and two lactating.

REMARKS—Hutterer (1986) considered *C. tansaniana* to be part of the *C. monax* group but differentiated the former from *C. monax* sensu stricto in being larger, with a more robust skull, and a more prominent third upper molar; no statistical comparisons of these parameters were presented in his description. With the increased sample sizes associated with our inventories, including new material of *C. monax* from Mt. Kilimanjaro (type locality), such statistical comparisons are now possible. A one-way ANOVA found few significant differences between sexes in cranio-dental characters for *C. monax* from Mt. Kilimanjaro (16 females, 48 males) and for *C. tansaniana* (12 females, 15 males); the significant values were for nasal width and mastoid plate, which may be best allocated

TABLE 8. Comparison of cranio-dental measurements between samples of *Crocidura monax* from Mt. Kilimanjaro and West Usambara and *C. tansaniana* from East Usambara, with results of a one-way ANOVA to test for significant differences among localities.

	KILI			WU			EU			F
	Mean ± SD	Range	n	Mean ± SD	Range	n	Mean ± SD	Range	n	
CI	23.2 ± 0.48	22.3–24.1	54	23.7 ± 0.46	22.9–24.7	18	25.1 ± 0.48	23.8–26.1	35	164.1**
BL	21.0 ± 0.43	20.3–21.9	54	21.4 ± 0.44	20.8–22.4	18	22.8 ± 0.41	21.8–23.5	35	193.1**
PPL	10.6 ± 0.24	10.0–11.1	54	10.6 ± 0.28	10.0–11.1	18	11.4 ± 0.27	10.9–12.1	36	124.5**
UTRL	10.2 ± 0.20	9.7–10.6	54	10.5 ± 0.23	10.0–11.0	18	11.1 ± 0.21	10.7–11.5	36	192.7**
LIW	5.2 ± 0.14	4.8–5.5	54	5.1 ± 0.19	4.6–5.4	18	5.4 ± 0.23	5.0–6.0	37	29.7**
BW	7.1 ± 0.13	6.8–7.3	54	7.3 ± 0.16	7.1–7.6	18	7.7 ± 0.19	7.2–8.0	37	165.2**
NW	1.9 ± 0.10	1.6–2.1	54	2.1 ± 0.11	1.8–2.3	18	2.2 ± 0.10	2.0–2.4	35	91.0**
GW	10.4 ± 0.25	9.9–11.0	54	10.6 ± 0.29	10.0–11.0	18	10.9 ± 0.28	10.3–11.6	36	38.7**
PMH	7.0 ± 0.32	6.4–8.0	54	6.9 ± 0.25	6.3–7.4	18	7.0 ± 0.20	6.6–7.5	36	0.9
M&I	14.8 ± 0.35	14.0–15.5	54	15.0 ± 0.42	14.0–15.7	18	16.0 ± 0.32	15.2–16.7	37	136.1**
LTR	9.5 ± 0.18	9.0–9.8	54	9.7 ± 0.24	9.1–10.3	18	10.3 ± 0.18	9.9–10.7	37	183.2**
I3W	0.80 ± 0.03	0.71–0.87	54	0.96 ± 0.05	0.80–1.02	18	0.98 ± 0.04	0.90–1.07	37	281.7**
CW	0.90 ± 0.04	0.80–0.97	54	1.00 ± 0.06	0.80–1.05	18	1.01 ± 0.04	0.93–1.10	37	86.4**
M3L	1.57 ± 0.06	1.44–1.69	54	1.71 ± 0.06	1.59–1.79	18	1.71 ± 0.06	1.60–1.93	37	73.4**
M3W	0.84 ± 0.04	0.74–0.95	54	0.87 ± 0.06	0.75–0.98	18	0.86 ± 0.05	0.74–0.97	37	4.3*
MAST	1.00 ± 0.11	0.75–1.31	54	1.19 ± 0.09	1.06–1.40	18	1.23 ± 0.12	0.90–1.42	36*	50.8**

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

to type II error. Hence, in both species the sexes were pooled for comparisons between the East Usambara (*C. tansaniana*) and the West Usambara/Mt. Kilimanjaro (*C. monax*). As noted above (see account of *C. monax*), animals from the West Usambara are significantly larger in most cranial dimensions than those from Mt. Kilimanjaro.

Table 8 lists the summary statistics of cranio-dental measurements for each of the three localities (East and West Usambaras and Mt. Kilimanjaro) and the F values for a one-way ANOVA to test for significant differences among populations. F values used to test the null hypothesis of no significant difference among the three localities were all highly significant (Table 8), with the greatest amount of morphological heterogeneity exhibited by characters of the upper toothrow and individual teeth. The highest F value exhibited was for the width of the third upper incisor (I^3-W). *Crocidura tansaniana* was the largest in every character measured, except width of the third upper molar (M^3W), which, for the West Usambara population of *C. monax,* was slightly larger. Hutterer's (1986) appreciation for the more robust nature of the skull in *C. tansaniana* was borne out in our analyses. The taxonomic implications of these observations are currently being examined using samples of *C.* cf. *monax* from other Tanzanian montane localities (Stanley, unpubl. data).

SPECIMENS EXAMINED—**EAST USAMBARA**, 6 km NW Amani, Monga Tea Estate (PF 19—FMNH 149961); 4.5 km WNW Amani, Monga Tea Estate, EU control site (PF 14—FMNH 147211, 147360; PF 31—FMNH 149976; PF 32—149969, 149971, 149972, 150375; PF 33—FMNH 149970; PF 58—FMNH 151106, 151108, 151376, 151380; PF 60—FMNH 151124; PF 61—FMNH 151121; PF 62—FMNH 151109, 151110, 151379, 151382; PF 63—FMNH 151107, 151123, 151125, 151377, 151378, 151381; TRL AO—FMNH 151111, 151120, 151122); 4.5 km ESE Amani, Monga Tea Estate, EU control site (PF 39—FMNH 149973; PF 42—FMNH 149974, 149975, 149978; PF 46—FMNH 149977; PF 65—FMNH 151112; PF 67—FMNH 151113, 151127; PF 68—FMNH 151132; PF 69—FMNH 151114–151116, 151118, 151119, 151126, 151128–151131, 151133, 151134; TRL AG—FMNH 150376; TRL AP—FMNH 151117).

Crocidura usambarae Dippenaar, 1980

DISTRIBUTION—*Crocidura usambarae* was described by Dippenaar (1980) based on specimens collected in the Shume and Magamba Forest Reserves of the West Usambara Massif, in the elevational range of 1580–1830 m. Two specimens without skulls from the Ngozi Crater, Poroto Mountains, in the Southern Highlands of Tanzania were tentatively referred to this species by Dippenaar (1980) based on pelage. The presence of this species in the Southern Highlands needs to be confirmed.

ECOLOGY AND REPRODUCTION—The type locality for *C. usambarae* is the West Usambara, in a zone between 1580 and 1830 m. During our study of small mammals of this massif, working sites between 1170 and 1300 m, we did not trap a single individual of this species during an accrued 7224 sample-nights. The only specimen we obtained was at 1050 m in the East Usambara, based on 11,339 sample-nights. This may be associated with this species' apparent preference for higher elevations. Stanley et al. (1996) documented more than twice as many individuals of this taxon at 2000 m than at 1100 m in the Chome Forest Reserve of the South Pare Massif, a site about 80 km from the holotype locality and separated by a valley descending to 400 m. The East Usambara specimen was taken in an overgrown agricultural area between a tea plantation and a stream running along the edge of the southeastern portion of the EU control area. It was a nulliparous sub-adult female.

SPECIMENS EXAMINED—**EAST USAMBARA**, 4.5 km ESE Amani, Monga Tea Estate, EU control site (PF 70—FMNH 151135).

Suncus megalura (Jentink, 1888)

DISTRIBUTION—*Suncus megalura* is found throughout tropical Africa, including savannah habitats (Hutterer, 2005). Oguge et al. (2004) documented this species at 2200 m in the

TABLE 9. Testis length and width for *Sylvisorex howelli* captured in the West Usambara between 1991 and 1993.

	1991 (n = 1)	1992 (n = 17)		1993 (n = 11)		Total (n = 29)	
		Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
Testes length (mm)	5	3.6 ± 0.50	3–4	3.6 ± 0.44	3–4	3.6 ± 0.53	3–5
Testes width (mm)	3	2.2 ± 0.39	2–3	2.0 ± 0.00	2–2	2.1 ± 0.35	2–3

isolated Mbololo Massif of the Taita Hills, but did not find it in other forests of that Kenyan mountain range.

ECOLOGY AND REPRODUCTION—Hutterer (2005) stated that this species is common at forest edges and in forested savannas. Our data support these habitat preferences, in that most specimens were captured in thick vegetation at the ecotone between forest and agricultural land. Only male *S. megalura* were trapped in the East Usambara (n = 3), and 12 of the 17 individuals collected in the West Usambara were male. Of the remaining five specimens, four were female and the sex of one was not determined. Three of the females were examined for reproductive condition; two were pregnant, each with a single embryo and crown–rump lengths of 16 mm (25 July 1991) and 3 mm (29 August 1992).

SPECIMENS EXAMINED—**EAST USAMBARA**, 6 km NW Amani, Monga Tea Estate (TRL W—FMNH 150379); 4.5 km WNW Amani, Monga Tea Estate, EU control site (PF 62—FMNH 151156); 4.5 km ESE Amani, Monga Tea Estate, EU control site (PF 70—FMNH 151157); **WEST USAMBARA**, 14.5 km NW Korogwe, Ambangulu Tea Estate (PF 6—FMNH 147373); 12.5 km NW Korogwe, Ambangulu Tea Estate (PF 1—FMNH 147188, 147189, 147367–147369, 147372; PF 2—FMNH 147371; PF 3—FMNH 147190, 147390; PF 48—FMNH 150037–150039); 11 km NW Korogwe, Ambangulu Tea Estate (PF 10—FMNH 147191, 147374; PF 13—FMNH 147192, 147375).

***Sylvisorex howelli* Jenkins, 1984**

DISTRIBUTION—Jenkins (1984) described *Sylvisorex howelli* based on specimens obtained in the Uluguru Mountains. Subsequently, Hutterer (1986) named the subspecies *S. h. usambarae* from the West Usambara. Stanley et al. (1998), Stanley and Olson (2005), and Stanley (unpubl. data) added five massifs to the known distribution of this shrew, endemic to the Eastern Arc—East Usambara, Nguru, Ukaguru, Nguu, and Rubeho Mountains. Thus, *S. howelli* is found only in the center massifs of the Eastern Arc Mountains. Even after extensive small mammal surveys with pitfall lines in the South and North Pare Mountains, the Udzungwa Mountains, and the Southern Highlands (Stanley et al., 1996, 2005b, 2007b; Stanley & Hutterer, 2007; Stanley, unpubl. data), this species is unknown south of the Ruaha River and north of the West Usambara.

ECOLOGY AND REPRODUCTION—*Sylvisorex howelli* has only been found in montane forests. In most cases, this species is among the most commonly collected shrews during faunal inventories (Stanley & Olson, 2005; Stanley, unpubl. data)—for example, 66.0% of the total trapped shrews in the West Usambara Mountains between 1991 and 1993. In contrast, two individuals of this species (1.4% of total shrews captured) were captured in the East Usambara over this three-year study. The ratio of females to males in the West Usambara was 2/2, 14/22, and 8/14, for 1991, 1992, and 1993, respectively. Of 16 females examined over three years, only one obtained in 1992 was pregnant, with a single embryo in each uterine horn, the largest of which had a crown–rump length of 3 mm. Table 9 reports testis measurements of *S. howelli*.

REMARKS—Stanley and Olson (2005) found that specimens from the East Usambara were smaller than those from the West Usambara, Nguru, Nguu, Uluguru, and Ukaguru Mountains. This pattern was not concordant in the concomitant molecular study based on mitochondrial DNA. The genetic data indicate that the East and West Usambara populations are sister groups, relative to all other Eastern Arc Mountain populations. Stanley and Olson (2005) hypothesized that the co-occurrence of *S. howelli* and the similar sized *Crocidura hildegardeae* in the East Usambara caused character displacement that led to smaller skulls in the local population of *S. howelli*.

SPECIMENS EXAMINED—**EAST USAMBARA**, 4.5 km ESE Amani, Monga Tea Estate, EU control site (PF 40—FMNH 150023; PF 45—FMNH 150008); **WEST USAMBARA,** 12.5 km NW Korogwe, Ambangulu Tea Estate (PF 5—FMNH 147184–147187; PF 49—FMNH 150009, 150013, 150018, 150026, 150032, 150034, 150035; PF 50—FMNH 150001, 150010, 150016, 150017, 150020, 150021, 150031, 150033, 150036, 150382, 150383; PF 51—FMNH 150011, 150012, 150014, 150015, 150019, 150024, 150025, 150381, 150384; PF 52—FMNH 150007, 150022, 150027–150029, 150387–150389; PF 53—FMNH 150030; PF 71—151144, 151151, 151387; PF 72—FMNH 151139, 151145, 151146, 151148, 151152, 151155; PF 73—151141, 151143, 151147, 151153, 151383, 151385, 151386; PF 74—FMNH 151140, 151142, 151149, 151150, 151154, 151384).

Macroscelididae

***Petrodromus tetradactylus* Peters, 1846**

DISTRIBUTION—The genus *Petrodromus* is represented by a single species, *P. tetradactylus*, and is distributed from southeastern Kenya to northeastern South Africa (Schlitter, 2005). Kingdon (1974) lists two subspecies occurring in Tanzania: *rovumae* and *tetradactylus*. In contrast, Jennings and Rathbun (2001) list three subspecies for the country—*rovumae*, *sultan*, and *zanzibaricus*—and illustrate a zone of overlap and possible hybridization between *P. t. sultan* and *P. t. rovumae* in northeastern Tanzania. Pelage characteristics identify the specimen collected during this study as *P. t. sultan*. Specifically, the reddish-brown dorsal stripe is clearly defined, distinct from the more lateral gray pelage, and the mid-ventral caudal bristles are long (4–5 mm) and all knobbed (Corbet & Neal, 1965).

ECOLOGY AND REPRODUCTION—This species is typically associated with dense vegetation, in both xeric and mesic habitats. In montane areas, *P. tetradactylus* is restricted to drier forests and is not found above approximately 1400 m (Jennings & Rathbun, 2001). It is often sympatric with the macroscelidid *Rhynchocyon petersi* Bocage, 1880, and we found both species in sympatry in the East Usambara. One female *P. tetradactylus* was collected 6 August 1993 at 0930 h

at the edge of the northeastern portion of the EU control site and in the ecotone between forest and tea plantation. External measurements are given in Table 3.

Remarks—Field workers from Frontier-Tanzania obtained a female (FMNH 182578) and a skull (FMNH 187089) 24 October 1996 in the Kwamgumi Forest Reserve, a lowland forest at 300 m near the base of the East Usambara Mountains and approximately 25 km NE of Amani (Doggart et al., 1999). N. J. Cordeiro collected a female and a male in the Bombo East I Forest Reserve at approximately 400 m between 17 and 21 September 1996 (FMNH 163412, 163413). These specimens also possess the knobbed long bristles on the ventral side of the tail and distinct dorsal brown stripe of *P. t. sultan*.

Specimens Examined—**EAST USAMBARA**, 4.5 km WNW Amani, Monga Tea Estate, EU control site (collected by hand—FMNH 151459).

***Rhynchocyon petersi* Bocage, 1880**

Distribution—The genus *Rhynchocyon* is more restricted in its distribution than the often-sympatric genus *Petrodromus*. *Rhynchocyon petersi* is documented from various localities across northeastern Tanzania, including the Nguru, East and West Usambara, and North and South Pare Mountains (Stanley et al., 1996, 2007b; Stanley, unpubl. data).

Ecology and Reproduction—Although *R. petersi* was not directly observed during the Usambara Mountain surveys of 1991–1993, a male was found dead in 1996 by W. D. Newmark in a snare set near the site of trap line A in the WU control area.

Remarks—Field workers from Frontier-Tanzania found a dead male on the road near the Kwamgumi Forest Reserve (FMNH 158851), a lowland forest at 300 m near the foot of the East Usambara Mountains, approximately 25 km NE Amani.

Specimens Examined—**WEST USAMBARA**, 12.5 km NW Korogwe, Ambangulu Tea Estate (proximity of TRL A—FMNH 158276).

Discussion

Faunistics

The soricid fauna of the East and West Usambara Mountains—The shrew fauna of both the East and West Usambara Mountains is diverse, especially in relation to other regional montane localities (see below). On each massif of the Usambaras, we collected species that occurred almost exclusively in forested habitats and others that were found predominately in more open or very disturbed forest habitats. Examples of species found almost exclusively in forest include *Crocidura hildegardeae*, *C. monax*, *C. tansaniana*, and *Sylvisorex howelli*. The single exception was a *C. hildegardeae* caught in a pitfall line set between a tea plantation and thick herbaceous/woody vegetation along a stream bank. This site was less than 30 m from the edge of the EU control site forest. Not only were these species generally restricted to forest sites, but also 98%, 88%, 98%, and 100% of specimens captured for *C. hildegardeae*, *C. monax*, *C. tansaniana*, and *S. howelli*, respectively, came from the control sites of the East and West Usambaras. Hence, these species are generally not present in the small forest parcels falling into the same elevation ranges as the control sites.

Conversely, other species (*C. elgonius*, *C. hirta*, and *C. jacksoni*) were found almost exclusively in non-forest habitats, including tea plantations, agricultural land, and secondary vegetation. Only one of the nine *C. elgonius* collected in the East Usambara was in relatively undisturbed forest; the rest were taken in tea plantations and agricultural habitat. In the West Usambara, four *C. elgonius* were collected in tea and *Eucalyptus* plantations, and only one specimen was taken in forest, in this case in the 37.8-ha site. This species was the most common of the mammals collected in tea plantations. *Crocidura hirta* was found in tea plantations, agricultural areas, and disturbed forest within fragments of less than 10 ha, with one exception in the East Usambara in the 29.4-ha fragment. The single record of *C. jacksoni* documented during this survey was in bamboo of a marshy area with some agricultural activities. This species is known from drier habitats in Tanzania, such as Tarangire National Park (Stanley et al., 2007c). All non-forested habitats sampled during our surveys were the result of human alteration of the natural vegetation. No natural savannah or other drier habitats occur in the portions of the Usambara Mountains we inventoried. Thus, we hypothesize that species such as *C. elgonius* and *C. hirta* arrived in the specific sampled areas after human modification of natural habitats. Whether the agent was natural colonization from more lowland areas or physical introduction by humans will require further study.

Differences between the East and West Usambaras—More shrew species were documented in the East Usambara Mountains (10) than in the West Usambara Mountains (6). In certain cases, a given taxon occurred on one massif and not the other, or was seemingly rare on one massif compared with the other based on our trap captures. For example, *C. monax* was only found in the West Usambara, and *C. hildegardeae*, *C. tansaniana*, and *C. usambarae* were found only in the East Usambara. *Sylvisorex howelli* was ubiquitous in the WU control area, but only collected twice (2% of all *S. howelli* captured) in the East Usambara. Most of the *C. hirta* we trapped came from disturbed habitats in the East Usambara. Differences in the shrew faunas between the two massifs may relate to elevational zonation, as most of our trapping efforts in the West Usambara were around 1300 m and in the East Usambara between 900 and 1100 m.

Regional differences of the Tanzanian northern massifs—The shrew fauna of the East and West Usambara Mountains is rich and diverse relative to those of other regional mountains, both geographically close (e.g., North and South Pares, Mt. Kilimanjaro) or geologically similar, with the same base rock composition (Uluguru). Surveys in the South and North Pare Mountains, using the same methodology during the same season, documented four and three shrew species, respectively, in the elevational range of 1100–2000 m (Stanley et al., 1996, 2007b). Despite a broader elevational range, this is less than 50% of the shrew species in the East Usambara and less than 70% of those in the West Usambara. There were also differences in measured abundance of some species. *Crocidura usambarae* made up 8.1% and 21.3% of the total number of shrews collected at 1100 and 2000 m, respectively, in the survey of the South Pare (Stanley et al., 1996), but it comprised only 0.7% of the total shrews taken in the East Usambara and was not trapped in the West Usambara Mountains.

Comparisons within and between Different Communities of Insectivorous Small Mammals in the Afrotropics and Madagascar

Over the past few decades, S.M.G. and W.T.S. have performed detailed inventories of insectivorous small mam-

mals in the Afro-Malagasy region using comparable field methods, particularly pitfall lines, and similar styles of installation and maintenance. Sufficient data are now available to make some first-order comparisons of species richness and diversity among different sites in the Afrotropics and Madagascar, with particular emphasis on levels of endemicity (Table 10). Madagascar sites are all in the eastern humid forests; those from the Afrotropics range from montane forest habitats to lower lying, less mesic forests.

On Madagascar, most insectivorous small mammals are of the endemic Family Tenrecidae (Order Afrosoricida), with the most speciose group being the shrew tenrecs, genus *Microgale*, of the Subfamily Oryzorictinae. This family contains 32 living species, most weighing less than 45 g (Goodman et al., 2008; Olson et al., 2009). In addition, two species of the Family Soricidae occur on Madagascar; one is introduced, and the indigenous status of the other is ambiguous (Hutterer & Trainer, 1990; Hutterer, 2005). Across the Afrotropics, the principal group of insectivorous small mammals are shrews Family Soricidae, with approximately 150 species known in this zone (Hutterer, 2005; Hutterer et al., 2009; Hutterer & Montermann, 2009; Kerbis Peterhans et al., 2008, 2009; Kerbis Peterhans & Hutterer, 2009; Mukinzi et al., 2009).

Notably, the insectivorous small mammal communities, soricid shrews for the Afrotropics and tenrecs for Madagascar, are not phylogenetically closely related (Murphy et al., 2001). Each lineage represents a separate adaptive radiation (although there is some paraphyly within Afrotropical soricids [Dubey et al., 2008]), and there are extraordinary levels of morphological convergence between the two groups. Hence, the Afro-Malagasy comparisons presented here allow an assessment of the evolution of ecological constraints between independently evolved lineages of insectivorous small mammals, with regards to models of speciation, the number of sympatrically occurring taxa, and patterns of endemism.

Although the Afro-Malagasy comparisons are insightful concerning the evolution and levels of speciation in these different insectivorous small mammal communities, some caveats are needed. Madagascar, with a total surface area of 581,500 km^2, has been isolated from other large landmasses for well over 120 million years (de Wit, 2003), and it has been estimated that the colonizing ancestor of the Tenrecidae arrived between 42 and 25 million years ago (Poux et al., 2005). In contrast, tropical Africa is a vast expanse of about 20 million km^2 (Baccini et al., 2008), with a very complex geological history (e.g., Moore & Cotterill, 2010), resulting in different patterns of isolation and subsequent speciation of soricid shrews. This group apparently evolved in the Upper Miocene, is of Palearctic-Oriental origin, and colonized the African continent an estimated 1–5 million years ago (Dubey et al., 2008).

Given the different evolutionary histories of shrews and tenrecs, as well as the contrasting surface area and geological history of tropical Africa and Madagascar, meaningful comparisons using estimates of endemism can be problematic. To address these issues, we use three different measures here: (1) species endemic to a specific massif (=micro-endemic), (2) those restricted to a geographical region involving only a few neighboring massifs, and (3) those restricted to a specific phytogeographical zone (see Table 10, footnote 1). The sites chosen for Madagascar are massifs with montane forest that are isolated from one another by other types of lower lying forest formations and, hence, are in parallel with the definition number 2 presented above. Finally, with one exception (Central African Republic), the data used in these comparisons came solely from surveys designed and conducted by W.T.S. or S.M.G., who employed largely consistent field methodologies (Table 10).

Intra-Afrotropical comparisons—In comparing the species richness among various small insectivore communities (shrews) within the Afrotropics, several patterns emerge (Table 10). The submontane and montane (sensu Lovett & Pócs, 1993) forests of the Eastern Arc Mountains in northern Tanzania (East and West Usambara and South and North Pare Mountains), spanning the latitudinal range from 3°S to 5°S, show notable differences in species richness; the Usambaras have 6–10 species and the Pares 3–4 species. The elevational range each massif presents and its distance to the coast may in part explain the differences in species richness; elsewhere, both factors, as well as aspect, affect orographic precipitation and the length of the dry season (Basist et al., 1994; Abebe & Savenije, 1995). The summits of the East and West Usambara Mountains reach 1506 and 2200 m, respectively, and these massifs are 50 and 100 km, respectively, from the Indian Ocean coast. In contrast, the South and North Pares have summits at 2463 and 2113 m, respectively, and are 150 and 220 km, respectively, from the coast. The Pares are, in part, in the rain shadow of the Usambara Mountains and, to a smaller extent, in that of the Taita Hills of southern Kenya. Mount Kilimanjaro, with a different geological origin, composition, and age, with six species of small insectivorous animals and several different types of natural habitats, is a further example of this pattern; this massif lies to the northwest of the Pares and rises to 5895 m, and the eastern flank is 275 km from the coast.

In contrast to species diversity, insectivore endemism is largely consistent across these four Eastern Arc Mountains, based on the phytogeographical zone endemism classification (see Table 10, footnote 1) with respect to the Tanganyika Montane Forest Group. They range from 25% in the South Pare, to 30% in the East Usambara, to 33% in the North Pare and West Usambara. The shrew fauna of Mt. Kilimanjaro shows 33% endemism based on this definition. From a regional perspective, the percentage of species found on these mountains, and only a few other nearby montane localities, ranged from 0% on the North Pare to 25% on the South Pare; figures for the Usambaras and Mt. Kilimanjaro are intermediate (Table 10).

In the southern Eastern Arc Mountains, across the latitudinal gradient from 6.5°S to 8.5°S, shrew species richness is reduced, with four and five taxa per massif in the Uluguru and Ukaguru, respectively. The summits of these mountains are at 2400 and 2250 m, respectively, and the distances to the coast are 180 and 220 km, respectively. The exception to the relatively low shrew taxonomic diversity in the southern Eastern Arc Mountains is the Udzungwa Massif. This massif, with 10 species, rises to 2580 m, and the eastern flank is 300 km from the coast. Differences in species richness among these three massifs appear to correlate with their position relative to the Indian Ocean and general topography, which in turn would be associated with orographic precipitation, surface area of each massif, and the elevational range sampled. Relative to the Uluguru and Ukaguru, the Udzungwa Massif is the largest of the Eastern Arc Mountains, and no other geological feature blocks the passage of weather systems arriving from the Indian Ocean. Contrasting insectivore

TABLE 10. Comparisons of patterns of species richness of insectivorous small mammals at different sites in the Afro-Malagasy region. Habitat classifications are based on Lovett and Pócs (1993) for the Afrotropics and Du Puy and Moat (1996) for Madagascar. Site names in bold are part of the Eastern Arc Mountains (Lovett, 1990).

Site (Country)	Elevation (m) (range of survey)	Trapping type and effort			Habitat type	Latitude (centroid)	Species richness	Different measures of % endemism[1]	Source of data[2]
		Bucket-nights	Trap-nights	Sample-nights					
East Usambara (Tanzania)	900–1110	3314	8025	11,339	Submontane forest	5°3′S	10	10–20–30	1
West Usambara (Tanzania)	1120–1300	1924	5300	7224	Submontane forest	5°3′S	6	0–16–33	1
South Pare (Tanzania)	1100–2000	1364	3794	5158	Submontane forest	4°18′S	4	0–25–25	2
North Pare (Tanzania)	1550–1700	1089	2286	3375	Submontane forest, with some fragmentation	3°34′S	3	0–0–33	3
Udzungwa (Tanzania)	600–2000	2893	7448	10,341	Dry submontane to montane forest	8°23′S	10	10–30–50	4
Minziro (Tanzania)	1150	550	1505	2055	Guineo-Congolian lowland forest	1°1′S	6	0–0–0	5
Uluguru (Tanzania)	1350–1850	1739	5620	7359	Submontane to montane forest	6°55′S	4	0–75–100	6
Ukaguru (Tanzania)	1800–1900	1727	3134	4861	Submontane to montane forest	6°22′S	5	0–60–80	6
Mt. Kilimanjaro (Tanzania)	2000–4000	3201	8361	11,562	Submontane forest to alpine desert	3°10′S	6	17–17–33	6, 7
Mt. Mulanje (Malawi)	1000–1850	1320	2608	3928	Submontane forest to montane grassland	15°58′S	3	0–0–0	6
Minkébé (Gabon)	600	330	1500	1830	Guineo-Congolian lowland forest	2°5′S	11	0–0	8
Mt. Doudou (Gabon)	110–625	726	1650	2376	Lowland rain forest to mid-elevation rain forest	2°15′S	9	0–0	9
Dzanga-Sangha and Dzanga-Ndoki forests (Central African Republic)	300–650	All identified species were identified from remains in small carnivoran scats.			Semi-deciduous	2°30′N	17	6.5–13	10
Anjanaharibe-Sud (Madagascar)	875–1550	814	1646	2460	Undisturbed lowland and montane forest	14°45′S	11	9–73	11
Marojejy (Madagascar)	775–1625	726	2100	2826	Undisturbed lowland and montane forest	14°30′S	14	7–79	12
Tsinjoarivo (Madagascar)	1400–1550	396	1200	1596	Montane forest slight degradation and some fragmentation	19°45′S	15	0–87	13
Ambohitantely (Madagascar)	1450–1660	627	1750	2377	Fragmented montane forest	18°20′S	10	0–70[3]	14
Andringitra (Madagascar)	810–1625	902	1925	2827	Undisturbed lowland and montane forest	22°15′S	13	0–77	15

[1] We provide three separate measures of endemism, which are, in order: (1) micro-endemics or strict endemic, which refers to a species not known outside of the specific site or massif; (2) regional endemics, which is defined as taxa that have limited geographical ranges, including the specific study site (such as certain massifs in the Eastern Arc Mountains and nearby massifs). For Madagascar, these comparisons are limited to the eastern humid forests; (3) phytogeographical zone endemics, for Eastern Arc Mountains and some other sites ranging from Tanzania to southern Malawi, shrews endemic to the Tanganyika Montane Forest Group (sensu Moreau, 1966), and Mt. Kilimanjaro. This phytogeographical region has been picked to make comparisons between this zone and Madagascar more equitable with regard to several different parameters.

[2] Data sources: 1 = herein; 2 = Stanley et al. (1996, 1998); 3 = Stanley et al. (2007b); 4 = Stanley and Hutterer (2007); 5 = Stanley and Foley (2008); 6 = W. T. Stanley (unpubl. data); 7 = Stanley et al. (2003); 8 = Goodman et al. (2001); 9 = Goodman and Hutterer (2004), Nicolas et al. (2004); 10 = Ray and Hutterer (1995), Lunde (2007); 11 = Goodman and Jenkins (1998); 12 = Goodman and Jenkins (2000); 13 = Goodman et al. (2000); 14 = Goodman and Rakotondravony (2000), Olson et al. (2004); 15 = Jenkins et al. (1996), Goodman and Rasolonandrasana (2001).

[3] This includes *Suncus madagascariensis*, which may not be endemic to Madagascar, but an introduced form of *S. "etruscus."*

endemism based on phytogeographical regions (see Table 10, footnote 1), the Uluguru (100%) and Ukaguru (80%) have notably high levels of small mammal endemism within the Tanganyika Montane Forest Group. In contrast, this value for the Udzungwa Mountains is only 50%. The regional endemics made up 60% and 75% of the Ukaguru and Uluguru samples, respectively, but only 30% of the Udzungwa samples.

Comparing other regional mountains with submontane forest to the Eastern Arc Mountains, sites such as Mt. Mulanje, summit at 3002 m in southern Malawi and forming the southern limit of the Tanganyika Montane Forest Group, has few shrew species and no regional endemics (Table 10). In the Guineo-Congolian forests near Minziro, in northwestern Tanzania, six species of shrew were recorded, none endemic. Portions of central western Africa, represented in our data set by Minkébé, Monts Doudou, and the Dzangha-Sangha/Dzanga-Ndoki complex, have high species richness, ranging from 9 to 16 taxa, with regional endemism ranging from 0% to 13%.

The highest measure of shrew species richness (Table 10) is the Dzangha-Sangha/Dzanga-Ndoki complex in the Central

African Republic, part of the Congo River basin. Here, where a marked dry season extends from December to March, 17 species of shrew were identified from small carnivore scats and some limited field surveys (Ray & Hutterer, 1995; Lunde, 2007). Whether Dzangha-Sangha/Dzanga-Ndoki has an exceptional diversity of small insectivorous animals or the lower measures of species richness at the other sites mentioned in Table 10 using the pitfall and trap techniques are artifacts of sampling techniques will require further research. Sites in Gabon within the same elevational range and habitat types as Dzangha-Sangha/Dzanga-Ndoki sampled by pitfall traps have notably lower measures of shrew species richness.

Intra-Malagasy comparisons—Five sites from the eastern humid formations of Madagascar, spanning the latitudinal range from about 14°S to 22°S, were compared with the Afrotropical sites (Table 10); four of these sites are large massifs that form separate montane forest islands, and the fifth is an isolated and fragmented series of forest parcels. In the four intact sites, where tenrec surveys were conducted in the same elevational range and forest type, species richness varied from 11 taxa at Anjanaharibe-Sud to 15 at Tsinjoarivo. The lowest species richness of the five sites was 10, recorded at Ambohitantely, the locality with heavy anthropogenic fragmentation. Only two of the five sites had micro-endemic taxa of tenrecs (Anjanaharibe-Sud and Marojejy Massifs), with values ranging from 7% to 9% of the total local fauna. Levels of endemism for each of these sites within the broader regional eastern humid forests ranged from 70% (Ambohitantely) to 87% (Tsinjoarivo).

Inter-Afrotropical–Malagasy comparisons—Except for two sites, more tenrec species occurred in the intact montane sites on Madagascar than did shrews in similar habitats in the Eastern Arc Mountains (Table 10). The exceptions are the East Usambara and Udzungwa Mountains; each had the same number of species as did Ambohitantely, the least diverse (10 taxa) of the Malagasy sites used in these comparisons. Ambohitantely is a fragmented montane forest with blocks ranging from 0.64 to 1250 ha and the local insectivorous small mammal community forms a nested subset, presumed to have undergone faunal collapse (Goodman & Rakotondravony, 2000). Notably, trapping effort was between four to five times greater at the East Usambara and Udzungwa Mountains than at Ambohitantely.

Table 10 presents several measures of endemism. The number of strict micro-endemics in the Eastern Arc Mountain and Malagasy montane forest sites differ little; the former ranges from 0% to 10% of the local insectivorous small mammal fauna being restricted to a specific massif and the latter from 0% to 9%. For the different surveyed sites in the Eastern Arc Mountains, the percentage of endemic species in the local community, when measured at the regional level, ranges from 16% to 75%, with the exception of the North Pare (0%). The comparisons at the phytogeographical level of the expanded Tanganyika Montane Forest Group show levels ranging from 30% to 100%. At several sites, such as the Uluguru and Ukaguru Mountains, species are relatively few, but most taxa are regional endemics. Probably the best comparison of these measures of endemism between the Eastern Arc Mountains and Madagascar is the number of species at a given site that are restricted to the eastern humid forest, where the values range from 70% to 87% (Table 10). Hence, at a regional level, the Tenrecidae show similar percentages of endemic taxa as the Soricidae in the Eastern Arc Mountains, despite tenrecs having been in place five times as long as the latter. Why faunas of significantly different geological ages show comparable endemism is not apparent and bears further investigation. Intervening habitats (humid forests versus drier woodland habitats), geological history, and timing of climatic perturbations and past connectivity of sites need to be taken into account. Another important consideration is the notable advancement of taxonomic work on tenrecs in the recent decades compared with Afrotropical soricids, particularly in this case, Eastern Arc shrews, which are still under scrutiny, and new species may be uncovered by ongoing molecular and morphological analyses.

As mentioned earlier, all of the members of the Tenrecidae are endemic to Madagascar. In the humid forests of the central and eastern portion of the island, most members of this family have broad distributions; few taxa are micro-endemics. An exception associated with the sites chosen here for comparison is *Microgale monticola*, which is only known from the Anjanaharibe-Sud and Marojejy Massifs (Goodman & Jenkins, 2000). At virtually all of the Malagasy sites inventoried, the number of sample nights exceeds 2300, which should provide a relatively precise measure of local species richness. The exception is at Tsinjoarivo, with slightly less than 1600 sample-nights, and the Malagasy site with the highest measure of species richness. The lowest species count is from the heavily fragmented forests of Ambohitantely. Across an assortment of different dry forests of western Madagascar, species richness of Tenrecidae is generally two to five species, but one site, Kirindy (CFPF), holds seven taxa (Soarimalala, 2008), notably less than the most species poor montane site in the east.

On the Tanzanian side, three species of shrew are known only from one mountain range (*Crocidura tansaniana*—East Usambara; *Congosorex phillipsorum*—Udzungwa; *Myosorex zinki*—Mt. Kilimanjaro). In addition, five species are restricted to a subset of mountain ranges within the Eastern Arc (*Crocidura desperata*, *C. telfordi*, *M. kihaulei*, *M. geata*, and *Sylvisorex howelli*). These distributions have been documented with intense surveys involving more than 3500 sample-nights at different montane sites. The one lowland Tanzanian site included in our comparisons is Minziro in the northwestern corner of the country and composed of Guinea-Congo habitat. In slightly more than 2000 sample-nights accrued at this sight, six species were documented, not one of which is locally endemic or regionally restricted.

Conservation

Tanzanian endemics such as *Crocidura monax*, *C. tansaniana*, and *Sylvisorex howelli* were found only in the forests of the control areas of the Usambara Mountains. These forest blocks are under constant threat from illegal logging and other influences, such as wind damage, invasive tree species (e.g., *Maesopsis*), and a variety of other human-induced pressures. Given that species such as *C. tansaniana* are found only in relatively pristine forest on the East Usambara Massif, and that the forests we sampled on the West Usambara Massif are the lowest remaining montane forests of that range, all remaining forest patches need to be conserved. The Amani Nature Reserve is a good example of the type of conservation actions that are regionally required to preserve the remaining montane forest habitats of the East and West Usambaras.

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Chapter 3

Small Mammal Inventories in the East and West Usambara and South Pare Mountains, Tanzania. 3. Chiroptera

William T. Stanley[1] and Steven M. Goodman[1]

[1]*Department of Zoology, Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, IL 60605 USA*

Abstract

Whereas the terrestrial mammal fauna of the East and West Usambara Mountains have been the subject of numerous investigations, the local bat fauna remains poorly documented, as is the case for bats of the South Pare Mountains. During mammal surveys of these three massifs, we used mist nets to collect local bats, documenting 20 bat species in total.

In the Usambara Mountains, 161 individual bats representing 19 species were documented during the three years of the survey between 1991 and 1993. In the East and West Usambara Mountains, 17 and 12 species, respectively, were recorded. Most animals were taken in net sets placed outside or at the edge of forested habitats. In the South Pare Mountains, 67 bats representing six species were collected during the two surveys, including 62 bats of six species at 1100 m (surveyed 17–29 July 1993) and five bats representing three species at 2000 m (surveyed 19–28 August 2004). Based on our morphological studies, no evidence of undescribed taxa in these collections exists.

Species common across all three massifs include two pteropodids (*Epomophorus wahlbergi* and *Lissonycteris angolensis*), one rhinolophid (*Rhinolophus clivosus*), and one vespertilionid (*Neoromicia capensis*). Taxa only captured on a single massif include *Rousettus lanosus* and *Rhinolophus simulator* (South Pare, 10% of total captures), *Myonycteris relicta* and *Nycteris thebaica* (West Usambara, 10% of total captures), and *Rousettus aegyptiacus*, *Rhinolophus deckenii*, *R. fumigatus*, *R. swinnyi*, *Nycteris grandis*, *Myotis bocagei*, and *Scotophilus viridis* (East Usambara, 35% of total captures).

Comparisons of capture rates and species richness between these three montane sites to more lowland forest sites indicate a notable reduction in species richness and density with increasing elevation. Our preliminary surveys are at best rough estimates of patterns of species diversity and richness in the montane portions of these massifs; more fieldwork and associated taxonomic work are clearly needed to have more in-depth knowledge of the local bat fauna.

Introduction

The bat fauna of Tanzania is diverse but poorly known (Monadjem et al., 2010). Studies of the country's bat fauna have discovered several species new to science in different habitats (Kock & Howell, 1988; Stanley, 2008), documented taxa that were previously unrecorded (Stanley & Foley, 2008), or collated and summarized information about a particular taxonomic group (Harrison, 1971; Bergmans, 1988, 1994, 1997; Csorba et al., 2003). Whereas the terrestrial mammal fauna of the Eastern Arc Mountains has been the subject of biological investigations for decades (see Stanley et al., this volume), the local bats have only recently been inventoried (Stanley et al., 2007a,b). Studies by Dieter Kock, in particular, largely based on specimens obtained by Kim Howell, highlighted aspects of this fauna (i.e., Kock & Howell, 1988; Kock et al., 2000); our knowledge of the fauna of montane habitats outside the Usambaras has also been augmented (Stanley et al., 2000, 2005a,b,c). During small mammal surveys in the East and West Usambaras (see Stanley et al., this volume) and South Pare Mountains (Stanley et al., 1996, 1998), we trapped and collected bats. Herein we present information on the bat taxa obtained and the associated natural history data from portions of the East and West Usambara Mountains and South Pare Mountains.

Study Area

Descriptions of our study sites in the montane portions of the East and West Usambara Mountains are presented in Stanley et al. (this volume). Specimens collected in the South Pare Mountains are from two localities: (1) Chome Forest Reserve, 7 km S Bombo, 4°20′S, 38°0′E, 1100 m (surveyed 17–29 July 1993) and 3 km E, 0.7 km N Mhero, 4°17′10″S, 37°55′40″E, 2000 m (surveyed 19–28 August 2004). Details of the ecological settings of these sites are given in Lovett and Pócs (1993) and Stanley et al. (1996, 1998). Both of the South Pare sites are submontane forests (sensu Lovett & Pócs, 1993), but the 1100-m site was notably drier than the 2000-m site.

Forested and agricultural sites on the Bulwa, Kwamkoro, and Monga Tea Estates in the East Usambara, and the Ambangulu Tea Estate in the West Usambara were sampled

between 1991 and 1993. Specific dates of surveys in the East Usambara were 05–09 August 1991, 19 July–24 August 1992, and 30 July–13 August 1993 and in the West Usambara were from 01–31 July 1991, 27 August–04 September 1992, and 18–22 August 1993.

Methodology

Capture Techniques

Although the chiropteran fauna was not the principal focus of our small mammal surveys in the montane areas of the East and West Usambara and South Pare Mountains, efforts were made to trap bats at the different inventory sites. Bats were captured using mist nets (12 m long, 3 m high, five-tiered) erected in an opportunistic manner in various settings, including over streams, across forest paths or near standing bodies of water. In the East and West Usambara Mountains, bats were occasionally found in nets (of the same dimensions) set by William D. Newmark for a project monitoring the effects of forest fragmentation on understory birds (Newmark, 1991, 2006). These nets, referred to herein as "bird nets", were set (parallel) along the central portion of cleared paths in the understory of different sizes of forest parcels, with the lowest rung touching the ground, and open from dawn to 1900 h.

Specimens and Taxonomy

Bat specimens were either prepared as skins with associated skulls and axial skeletons or fixed in formalin. Tissues, including heart, liver, and kidney, were frozen in liquid nitrogen. All specimens are deposited in the Field Museum of Natural History (FMNH), Chicago. We follow herein the taxonomy of Simmons (2005) for bats, except the genus *Miniopterus* is assigned to a separate family, the Miniopteridae (Hoofer & Van Den Bussche, 2003; Miller-Butterworth et al., 2007). FMNH catalogue numbers are presented for each voucher specimen.

Measurements

All measurements are in millimeters, except weight, which is in grams.

External Measurements—External measurements of collected specimens were made in the field before preparation following DeBlase and Martin (1974) using a plastic ruler marked in millimeters. The measurement methodology of each field worker varied in some cases. For this reason and similar problems highlighted by Blackwell et al. (2006), external measurement statistics are separated by collector.

TL	total length (from the tip of the nose to the last caudal vertebra)
HB	head and body length (from the tip of the nose to the junction of the tail and the body)
TV	length of tail vertebrae (from the junction of the tail and body to the last caudal vertebra)
HF	hind foot length (from the ankle to the tip of the longest claw for W.T.S.; ankle to insertion of claw for S.M.G.)
FA	forearm length (from outside edge of wrist to outside edge of the elbow of the folded wing)
EAR	ear length (from the notch at the base of the ear to the longest point of the ear)
TR	tragus length (from base to distal-most tip of tragus)
WT	weight (measured with Pesola scales)

Cranial Measurements—Cranial measurements were taken with digital calipers to an accuracy of 0.01 mm (by W.T.S.) on cleaned skulls of adult bats, defined as animals with a fully erupted third upper molar and the suture between the basioccipital and basisphenoid bones fused. These measurements vary between different genera and follow the definitions (but not necessarily the abbreviations) listed by Bergmans (1988) for *Epomophorus*, Kock et al. (2000) and Csorba et al. (2003) for *Rhinolophus*, and Bates et al. (2006) for vespertilionids.

ALSW	greatest width of the anterior lateral swellings on the rostrum of *Rhinolophus*
AMSW	greatest width of the anterior median swellings on the rostrum of *Rhinolophus*
BW	greatest width of braincase
CBL	greatest length from occipital condyles to front of premaxilla
CCL	greatest length from occipital condyles to anterior surface of upper canines
CIL	greatest length from occipital condyles to anterior-most point of upper incisors
CRN	greatest length from posterior-most point of cranium to front of premaxilla
GLS	greatest length from posterior-most point of cranium to anterior surface of upper canines
GSKL	greatest length from posterior-most point of occipital to anterior-most point of upper incisors
IOW	least interorbital width
LW	greatest breadth across rostrum at lachrymal projections
MAND con	greatest length from anterior-most point of the mandible (not including incisors) to the condyle
MAND ang	greatest length from anterior-most point of the mandible (not including incisors) to the most posterior end of angular process
MAND HT	the perpendicular greatest height of mandible, measured by placing the mandible on a microscope slide and measuring from the bottom of the slide to the top of the coronoid process and subtracting the thickness of the slide from the total
MAST	mastoid width
PAL	length of palate from posterior margin of the palate (at the median plane in Pteropodidae, to the side of any median projection in insect-eating bats) to the front of the premaxilla, or maxilla in *Rhinolophus*
POW	postorbital width
ROST	length of rostrum between anterior-most point of the orbit margin and the front of the premaxilla
ZYG	zygomatic width

Dental Measurements—

C-C cing	greatest distance from the labial side of the cingulum of one upper canine to the labial side of the cingulum of the other canine
C-C alv	greatest distance from the labial side of the alveolus of one upper canine to the labial side of the alveolus of the other canine

TABLE 1. Bat species represented by specimens collected during our surveys in the East and West Usambara and South Pare Mountains between 1991 and 1994. The two sites sampled in the South Pare Mountains differed in elevation by 900 m and are presented separately.

Species	East Usambara (900–1150 m)	West Usambara (1150–1300 m)	South Pare (1100 m)	South Pare (2000 m)
Epomophorus wahlbergi	X	X	X	
Lissonycteris angolensis	X	X	X	X
Myonycteris relicta		X		
Rousettus aegyptiacus	X			
Rousettus lanosus			X	
Rhinolophus clivosus	X	X	X	X
Rhinolophus deckenii	X			
Rhinolophus fumigatus	X			
Rhinolophus hildebrandti	X	X		
Rhinolophus simulator				X
Rhinolophus swinnyi	X			
Nycteris grandis	X			
Nycteris thebaica		X		
Glauconycteris argentata	X	X		
Myotis bocagei	X			
Scotophilus dinganii	X	X		
Scotophilus viridis	X			
Pipistrellus hesperidus	X	X		
Neoromicia nanus	X	X	X	
Miniopterus schreibersii	X	X		
Total no. of species	16	11	5	3

I^1-M^3 greatest length of upper toothrows, from the upper incisor to the last upper cheektooth measured at the alveoli

I_1-M_3 greatest length of lower toothrows, from the lower incisor to the last lower cheektooth measured at the alveoli

lowermols length of lower molariform toothrow

LUTR greatest length of upper toothrows, from the upper canine to the last upper cheektooth measured at the cingulum

LLTR greatest length of lower toothrows, from the lower canine to the last lower cheektooth measured at the cingulum

M^3-M^3 greatest distance from the labial side of the cingulum of one upper M^3 to the labial side of the cingulum of the other M^3

PAL/LUTR measured only in *Rhinolophus*; the length of the palate expressed as a percentage of the length of the upper toothrow (LUTR)

UPMOLS length of upper molariform toothrow

Locality Information

In Stanley et al. (this volume), we present detailed information on the different sites visited in the East and West Usambara Mountains. Here, we employ the site names mentioned in Stanley et al. (this volume), where details on the coordinates and elevations of the different surveyed sites can be found. Furthermore, information is repeated in the species accounts under the subheading "Specimens Examined", and the cited locality information is as originally inscribed in the field collector's catalog.

Results

Based on our morphological examination of the specimens collected, including comparisons to previously identified voucher specimens, no evidence was found that any of the bats obtained represent an undescribed taxon. However, undescribed cryptic species may be represented in the collection, particularly in genera such as *Rhinolophus* or *Pipistrellus*. Our chiropterological surveys of the South Pare, East Usambara, and West Usambara massifs provide new information on the locally occurring species, patterns of elevational variation, and insights into numerous aspects of their natural history.

South Pare Mountains

In the South Pare Mountains, 67 individual bats representing six species were collected during the two surveys: 62 bats of six species at 1100 m and five bats representing two species at 2000 m (Table 1), with six and two nights at each site (respectively) devoted to bat capture. Of the species obtained, the most numerous were *Lissonycteris angolensis* and *Rousettus lanosus*. At the 1100-m site, the net set that resulted in the highest capture rate was placed on an 18-m-long bridge spanning and approximately 6 m above the Mhokeveta River. At this site, relatively lush closed forest vegetation covered both banks, which created a tunnel-like overhang over the river and a natural flyway.

On several occasions, we found different bat taxa in the net at the same time, which had flown into the device from different directions. For example, on one night, 26 fruit bats were netted, consisting of 11 *L. angolensis* (seven females and four males) and 15 *R. lanosus* (12 females and three males). Although the synchronization of these captures may have been, in part, by chance, we suspect the alarm or distress calls of trapped individuals attracted other bats to the immediate vicinity that were then captured in the net. On several occasions we observed pteropodid bats tangled in the net and vocalizing, and almost immediately thereafter other fruit bats, sometimes of different genera, flew into the same net. For example, on 20 July 1993, at approximately 2000 h, a trapped *L. angolensis* vocalized and immediately singletons of *L. angolensis* and *Epomorphorus wahlbergi* flew into the net.

Usambara Mountains

In the Usambara Mountains, 161 individual bats representing 19 species were documented during the three years of the survey between 1991 and 1993. In the East and West Usambara Mountains, 16 and 11 species, respectively, were recorded (Table 1). Most of these animals were taken at sites outside or near the edge of forested habitats. Habitat settings in which bats were netted include next to reservoirs and cisterns, across small streams and marshy areas, ecotones between forest and agricultural areas, and inside forests.

Accounts of Species

The following accounts present information pertaining to the distribution, habitat, ecology, reproduction, specimens examined (including catalogue numbers, sites, and dates specimens were collected; see Stanley et al., this volume), and, when necessary, miscellaneous remarks.

Family Pteropodidae

Epomophorus wahlbergi (Sundevall, 1846)

Distribution—*Epomophorus wahlbergi* is distributed throughout sub-Saharan Africa, including much of Tanzania, although most records with associated vouchers are from the eastern half of the country. Bergmans (1988) cited specimens from Ambangulu, West Usambara. He also listed Amani, East Usambara, as a published locality but did not examine specimens from this site. We captured one adult specimen of *E. wahlbergi* in the South Pare Mountains, four at Ambangulu, and 23 at Amani.

Ecology and Reproduction—In the South Pare Mountains, one female was netted on 20 July 1993 over a small side channel of the Mhokevuta River in a zone where the river width was about 8 m. This specimen seemed to be attracted to the net by a vocalizing *Lissonycteris angolensis* that was already entangled. The *E. wahlbergi* specimen had large nipples, a perforate vagina, and an open pubic symphysis and was pregnant with one embryo in the right uterine horn with a crown–rump length of 17 mm.

The specimens collected in the East Usambara (EU) were taken in a variety of habitats, including at or just inside the forest edge, near standing water, and near tea plantations (see Stanley et al., this volume, for further details on the sites listed under "Specimens Examined"). Five animals (two females, three males) were netted in the ecotone between the control fragment and a tea plantation in a net set across a stream, one female was obtained at the edge of the Monga reservoir in a tea plantation, and one male was collected at a similar reservoir setting near Bulwa. Other sites where this species was collected include over a small cistern, with an opening measuring roughly 3 by 2 m, next to the Bulwa 2.6-ha fragment (one female); over a stream emerging from a marshy area near the village of Mbomole (one female, three males); and on the crest of a dam embankment next to a pond measuring approximately 40 by 80 m that was clogged with aquatic vegetation (three females, three males in 1992; two females, one male in 1993). Only two *E. wahlbergi* were captured inside natural forest, both in bird nets—one female in the 2.6-ha Bulwa fragment and one female near the start of the net line in the EU control site.

Eight female specimens from East Usambara from 1992 and 1993 were examined for reproductive activity, with four being pregnant and, in each case, with a single embryo. In three individuals, the embryo was in the left uterine horn and in one case in the right. The mean crown–rump length of the four embryos was 28.2 mm (SD = 5.4). In 1992, all pregnant specimens were captured between 30 July and 10 August, and in 1993, one pregnant female was collected on 2 August.

Two males and two females were obtained in the West Usambara (WU) during our study. One adult male was trapped in 1991 in the 5.5-ha fragment in a bird net about 1.5 m off the ground and about 25 m from the forest edge. The bat had abdominal testes measuring 6 by 4 mm, with non-convoluted epididymides. In 1992, three adult specimens were obtained in the control site—a male and a female collected at the forest edge and over a small shallow stream flowing out of the forest, and one female in a bird net in the WU control area. The male had testes measuring 7 by 6 mm with non-convoluted epididymides. One female had a slightly open pubic symphysis; the other had a closed symphysis. The nipples of both females were small.

In 1992, a female was netted between 1830 and 1950 h at the edge of a dammed pond in an agricultural area next to the village of Kazita within the Bulwa Tea Estate; other bats captured within an hour by the same net include *Rhinolophus fumigatus*, *Neoromicia nanus*, *Pipistrellus hesperidus*, and *Scotophilus dinganii*.

Comments—A one-way ANOVA was conducted on forearm length and the greatest length of skull to determine if size between the sexes was measurably different. Both measurements were significant (forearm length: $F = 13.4$, $P = 0.003$; skull length: $F = 20.0$, $P = 0.003$). Hence, descriptive statistics derived from external and cranio-dental measurements for each sex are presented separately (Tables 2 and 3).

Based on palatal ridge morphology, maxillary shape, and certain external measurements (Taylor & Monadjem, 2008; Monadjem et al., 2010), no evidence of *E. labiatus* or *E. crypturus* was found in the samples. *Epomophorus labiatus* is known from localities in northwestern and southwestern Tanzania, and *E. crypturus* from the southern portion of the country, but neither has been documented in northeastern Tanzania or the Eastern Arc Mountains (Bergmans, 1988).

Specimens Examined—**EAST USAMBARA**, 4.5 km ESE Amani, Monga Tea Estate, EU control site, 16–23 August 1992 (FMNH 150048–150050, 150397, 150398); 4.5 km WNW Amani, Monga Tea Estate, EU control site, 4–5 August 1992, 2–5 August 1993 (FMNH 150041, 150044, 150045, 150390–150396, 151179, 151180, 151413); 6 km NW Amani, Monga Tea Estate, 30 July 1992 (FMNH 150043); 8 km NWN Amani, Bulwa Tea Estate, 9–10 August 1992 (FMNH 150042, 150046, 150047); **WEST USAMBARA**, 11 km NW Korogwe, Ambangulu Tea Estate, 28 July 1991 (FMNH 147215); 12.5 km NW Korogwe, Ambangulu Tea Estate, WU control site, 1–2 September 1992 (FMNH 150399, 150400, 150051); **SOUTH PARE**, Chome Forest Reserve, 7 km S Bombo, 20 July 1993 (FMNH 151182).

Lissonycteris angolensis (Bocage, 1898)

Distribution—Bergmans (1994) recognized five subspecies of *Lissonycteris angolensis* distributed across western, central, and eastern Africa, and assigned specimens from eastern Africa to *L. a. ruwenzorii*, citing specimens from both Amani and Kwamkoro in the East Usambara. Simmons (2005) suggested that the *L. angolensis* complex may contain more

TABLE 2. External measurements (mm) and weight (g) of fruit bats (Pteropodidae) collected during 1991–1994 surveys of the East Usambara (EU), West Usambara (WU), and South Pare (SP) Mountains. Measurements were taken by both S.M.G. and W.T.S.

Species	TL	HB	TV	HF	EAR	FA	WT
Epomophorus wahlbergi W.T.S.							
♀ EU							
Mean ± SD	150.0 ± 1.41	146.0 ± 1.41	5.0 ± 1.41	21.0 ± 0.00	24.0 ± 1.41	83.5 ± 2.12	85.5 ± 13.44
Range	149–151	145–147	4–6	21–21	23–25	82–85	76–95
n	2	2	2	2	2	2	2
♂ EU							
Mean ± SD	157.3 ± 11.87	150.8 ± 10.05	5.3 ± 0.50	23.3 ± 0.96	24.8 ± 0.50	84.5 ± 4.43	98.8 ± 16.68
Range	142–170	137–160	5–6	22–24	24–25	79–89	75–114
n	4	4	4	4	4	4	4
Epomophorus wahlbergi S.M.G.							
♀ EU, WU, SP							
Mean ± SD	159.9 ± 4.58	157.0 ± 7.30	5.0	17.2 ± 0.70	24.9 ± 1.49	82.6 ± 1.98	88.5 ± 6.25
Range	150–166	149–165		16–19	22–27	78–85	76.5–97
n	10	4	1	14	14	14	14
♂ EU, WU							
Mean ± SD	174.8 ± 5.72	175.3 ± 7.51		18.6 ± 2.33	25.5 ± 1.20	86.0 ± 1.07	108.2 ± 8.93
Range	170–184	168–183		17–24	23–27	85–88	99.5–128
n	5	3		8	8	8	8
Lissonycteris angolensis ♀, ♂, EU, WU, SP							
W.T.S.							
Mean ± SD	135.8 ± 4.69	129.0 ± 3.46	8.5 ± 1.58	22.1 ± 1.73	24.2 ± 0.92	81.3 ± 1.77	73.8 ± 6.25
Range	130–145	125–135	5–10	20–24	22–25	79–84	64.5–86
n	10	7	10	10	10	10	10
S.M.G.							
Mean ± SD	143.5 ± 4.42	134	8.6 ± 1.95	18.2 ± 1.75	24.0 ± 1.05	81.1 ± 3.09	73.5 ± 6.99
Range	131–153		3–14	13–24	22–26	75–89	62–93
n	48	1	47	48	48	48	48
Myonycteris relicta ♀ WU							
S.M.G.							
Mean ± SD	130.5 ± 0.71		11.5 ± 0.71	17.0 ± 0.00	22.0 ± 0.00	72.0 ± 0.00	58.3 ± 3.18
Range	130–131		11–12	17–17	22–22	72–72	56–60.5
n	2		2	2	2	2	2
W.T.S.	127	117	10	18	21	75	56
Rousettus aegyptiacus S.M.G.							
♀ EU	147		15	17	23	92	94.5
♂ EU							
Mean ± SD	174.0 ± 4.58		11.0 ± 3.46	19.0 ± 1.00	24.0 ± 2.00	96.0 ± 2.65	142.7 ± 8.39
Range	169–178		9–15	18–20	22–26	94–99	133–148
n	3		3	3	3	3	3
Rousettus aegyptiacus W.T.S.							
♀ EU	158	140	15	25	22	95	97
Rousettus lanosus S.M.G.							
♀ Mean ± SD	163.2 ± 7.66		18.5 ± 1.44	18.4 ± 1.16	23.4 ± 1.31	90.7 ± 2.90	114.8 ± 12.02
Range	151–176		17–22	16–20	21–25	86–95	97–132
n	12		12	12	12	12	10
♂ Mean ± SD	164.7 ± 3.79		17.7 ± 1.53	19.0 ± 1.00	24.3 ± 2.08	93.0 ± 1.73	127.7 ± 5.03
Range	162–169		16–19	18–20	22–26	92–95	123–133
n	3		3	3	3	3	3
Rousettus lanosus W.T.S.							
♀	151	138	18	23	24	86	89

than one species, and at least one of these subspecies has been elevated to full species (*L. goliath*) by Monadjem et al. (2010).

ECOLOGY AND REPRODUCTION—Twelve (11 females and one male) and 20 (nine females and 11 males) specimens, were collected in the East and West Usambara Mountains, respectively. Nine females were examined for embryos; four collected 23 July 1991 and between 26 July and 2 September were not in active reproduction, and five collected 1 July 1991 and between 25 July and 5 August 1992 had one embryo each, with a mean crown–rump length (SD, range) of 4.8 mm (0.84, 4–6, n = 5). The six males examined for reproductive status had mean testes measurements of 7.3 mm (1.03, 6–9) by 4.8 mm (0.98, 4–6). The epididymides of three males collected in July 1991, July 1992, and August 1993 were convoluted, whereas the three other males obtained in July 1991 and August 1992 were not convoluted.

In the South Pare Mountains, 28 specimens were netted during the two surveys: 26 (nine males and 17 females) at

TABLE 3. Cranio-dental measurements of fruit bats (Pteropodidae) from both the East and West Usambaras.

Measurement	*Epomophorus wahlbergi* ♀ (n = 8)	*Epomophorus wahlbergi* ♂ (n = 5)	*Lissonycteris angolensis* ♀ (n = 8)	*Lissonycteris angolensis* ♂ (n = 5)	*Myonycteris relicta* ♀ (n = 3)[1]	*Rousettus aegyptiacus* ♀ (n = 2)	*Rousettus aegyptiacus* ♂ (n = 2)	*Rousettus lanosus* ♀ (n = 6)	*Rousettus lanosus* ♂ (n = 1)
CRN									
Mean ± SD	47.5 ± 1.59	51.6 ± 0.55	40.5 ± 0.86	40.5 ± 1.08	36.0 ± 0.40	40.8 ± 0.95	43.0 ± 0.67	41.8 ± 0.99	
Range	45.1–49.6	50.8–52.3	39.0–41.7	39.4–42.0	35.8–36.5	40.2–41.5	42.5–43.5	40.3–42.9	
CBL									
Mean ± SD	47.5 ± 1.59	51.6 ± 0.55	39.8 ± 0.77	40.0 ± 0.94	35.0 ± 0.40	39.7 ± 0.23	41.8 ± 0.62	40.0 ± 0.95	
Range	45.1–49.6	50.8–52.3	38.3–40.5	38.9–41.2	34.7–35.5	39.6–39.9	41.4–42.3	38.6–41.1	
ROST									
Mean ± SD	19.2 ± 1.05	21.0 ± 0.30	15.2 ± 0.45	15.1 ± 0.32	13.0 ± 0.25	15.4 ± 0.42	16.6 ± 0.47	16.8 ± 0.33	
Range	18.0–20.7	20.6–21.3	14.6–15.8	14.7–15.4	12.8–13.2	15.1–15.7	16.3–17.0	16.4–17.2	
PAL									
Mean ± SD	28.3 ± 1.11	30.7 ± 0.54	22.5 ± 0.32	22.5 ± 0.29	19.1 ± 0.55	22.6 ± 0.04	24.1 ± 0.69	21.8 ± 0.46	
Range	26.9–29.9	30.0–31.5	22.0–22.9	22.1–22.9	18.7–19.7	22.6–22.6	23.6–24.6	21.2–22.4	
BW									
Mean ± SD	16.9 ± 0.33	17.4 ± 0.18	15.8 ± 0.34	15.6 ± 0.38	14.9 ± 0.28	16.2 ± 0.66	17.5 ± 0.17	17.0 ± 0.38	16.8
Range	16.5–17.3	17.2–17.7	15.3–16.4	15.3–16.2	14.6–15.2	15.8–16.7	17.4–17.6	16.4–17.5	
IOW									
Mean ± SD	8.3 ± 0.29	9.1 ± 0.48	7.3 ± 0.20	7.1 ± 0.49	7.1 ± 0.11	8.1 ± 0.39	8.8 ± 0.11	7.7 ± 0.22	7.8
Range	7.7–8.7	8.2–9.6	7.0–7.5	6.4–7.7	6.9–7.2	7.8–8.3	8.7–8.9	7.5–8.1	
POW									
Mean ± SD	9.8 ± 0.52	9.9 ± 0.67	8.9 ± 0.69	8.5 ± 0.27	9.2 ± 0.68	8.6 ± 0.57	8.2 ± 0.45	9.8 ± 0.58	9.7
Range	9.0–10.3	8.9–10.7	7.9–10.1	8.2–8.9	8.7–10.0	8.2–9.0	7.9–8.5	8.9–10.5	
ZYG									
Mean ± SD	25.9 ± 0.56	27.5 ± 0.44	23.9 ± 0.72	24.0 ± 0.59	22.0 ± 0.05	23.5 ± 0.73	27.9 ± 0.62	24.0 ± 0.88	24.7
Range	25.1–26.6	27.1–28.1	22.5–24.7	23.1–24.6	21.9–22.0	22.9–24.0	27.5–28.3	22.5–25.0	
MAND con									
Mean ± SD	37.3 ± 1.08	41.2 ± 0.79	31.8 ± 0.67	31.6 ± 0.57	27.7 ± 0.40	32.5 ± 0.68	34.0 ± 0.12	32.5 ± 0.82	32.4
Range	35.8–39.2	40.4–42.4	30.9–32.6	31.0–32.5	27.4–28.2	32.0–32.9	34.0–34.1	31.6–33.6	
MAND ang									
Mean ± SD	36.3 ± 1.41	39.6 ± 0.87	30.3 ± 0.52	29.8 ± 0.51	26.2 ± 0.24	31.2 ± 1.08	32.4 ± 0.37	30.6 ± 0.84	30.3
Range	34.4–38.6	38.9–41.1	29.4–30.9	29.3–30.6	26.0–26.5	30.4–32.0	32.2–32.7	29.4–31.7	
MAND HT									
Mean ± SD	15.5 ± 0.43	17.3 ± 0.75	13.1 ± 0.65	13.3 ± 0.43	11.1 ± 0.48	12.1 ± 0.93	14.3 ± 0.23	11.8 ± 1.00	11.8
Range	14.9–16.2	16.5–18.1	12.2–14.1	12.7–13.9	10.7–11.6	11.5–12.8	14.1–14.4	9.9–12.7	
LUTR									
Mean ± SD	16.4 ± 0.54	17.8 ± 0.36	15.5 ± 0.49	15.6 ± 0.28	13.5 ± 0.32	15.7 ± 0.55	16.8 ± 0.03	14.7 ± 0.31	
Range	15.3–17.2	17.3–18.2	14.7–16.3	15.1–15.9	13.1–13.7	15.3–16.1	16.8–16.8	14.3–15.2	
C-C cing									
Mean ± SD	9.4 ± 0.28	10.5 ± 0.28	7.9 ± 0.26	7.7 ± 0.19	7.0 ± 0.15	8.0 ± 0.06	9.3 ± 0.30	8.7 ± 0.29	
Range	9.0–9.8	10.2–10.9	7.4–8.2	7.4–8.0	6.9–7.2	7.9–8.0	9.1–9.5	8.2–9.0	
C-C alv									
Mean ± SD	8.8 ± 0.29	9.9 ± 0.29	7.0 ± 0.19	6.9 ± 0.18	6.3 ± 0.03	7.3 ± 0.36	8.5 ± 0.27	8.2 ± 0.22	
Range	8.5–9.3	9.5–10.2	6.6–7.3	6.7–7.2	6.3–6.4	7.0–7.5	8.3–8.7	7.8–8.4	
LLTR									
Mean ± SD	18.3 ± 0.74	20.1 ± 0.52	16.9 ± 0.38	17.1 ± 0.32	13.3 ± 0.26	17.1 ± 0.73	18.4 ± 0.03	16.5 ± 0.43	
Range	17.3–19.8	19.4–20.8	16.2–17.3	16.8–17.5	13.1–13.6	16.6–17.6	18.4–18.4	16.0–17.2	

[1] For ZYG measurements of *M. relicta*, n = 2.

1100 m and two females at 2000 m. Of the eight females examined for reproductive status, seven were pregnant, all with one embryo in the oviduct: four in the right horn and three in the left horn. The six pregnant females collected at 1100 m between 18 and 23 July 1993 had mean embryo lengths of 5.5 mm (0.84, 4–6). One pregnant female was collected at 2000 m on 25 August 1994 with a single embryo measuring 20 mm in crown–rump length. Ten of the female specimens collected in July 1993 had open pelvic symphyses.

The nine male *L. angolensis* collected at the 1100-m site in the South Pare Mountains all had abdominal testes. The sexual organs of four animals were measured, with the testes length ranging from 3 to 8 mm and width from 2 to 6 mm; only one of the four had convoluted epididymides.

COMMENTS—Bergmans (1997) concluded that male *L. angolensis* skulls are slightly larger than females, whereas females have slightly longer forearms than males. A one-way ANOVA was conducted to test for significant differences in

cranio-dental measurements between sexes and samples from our East and West Usambara collections (only females were collected in the East Usambara). In contrast to the results of Bergmans (1997), not one of the cranio-dental measurements ($P \leq 0.05$) or forearm length ($F = 0.98$, $P = 0.33$; females = 79.4, males = 78.3) showed a significant difference between the sexes or populations from the Usambara Massifs. Hence, samples from both mountains and sexes are combined for external measurements (but presented separately for each collector; Table 2) and for the cranio-dental measurements (Table 3).

Lissonycteris can be differentiated from *Rousettus* by the presence of webbing between the toes, a collar of thick rough hair around the neck and chest in males, and a weak angle in the alveolar line between the third and fourth premolar (Bergmans, 1997).

Specimens Examined—**EAST USAMBARA**, 6 km NW Amani, Monga Tea Estate, 25–27 July 1992 (FMNH 150055–150057, 150059, 150402, 150403); 4.5 km WNW Amani, Monga Tea Estate, EU control site, 5 August 1992, 19 August 1993 (FMNH 150060–150062, 150404, 150405, 151388); **WEST USAMBARA**, 14.5 km NW Korogwe, Ambangulu Tea Estate, 23 July 1991, 29 August–2 September 1992, 19 August 1993 (FMNH 147219); 12.5 km NW Korogwe, Ambangulu Tea Estate, WU control site, 1–13 July 1991, 29 August–3 September 1992, 19 August 1993 (FMNH 147216–147218, 147377–147380, 147383–147385, 150058, 150063, 150064, 150401, 150406, 150407, 151159); **SOUTH PARE**, Chome Forest Reserve, 7 km S Bombo, 1100 m, 18–23 July 1993 (FMNH 151160–151170, 151389–151403); Chome Forest Reserve, 3 km E, 0.7 km N Mhero, 2000 m, 25–26 August 1994 (FMNH 153845, 153925).

Myonycteris relicta Bergmans, 1980

Distribution—This species was described by Bergmans (1980) based on a holotype from the Shimba Hills in Kenya, roughly 100 km from the eastern edge of the East Usambara, and the paratypes collected at Ambangulu in January 1900. Subsequent records from Tanzania include the Nguru Mountains in 1960 (Schlitter & McLaren, 1981), the Udzungwa Mountains in 1995 (Stanley et al., 2005b), and the East Usambara in Mgambo Forest Reserve at 400 m by N. J. Cordeiro (FMNH 163391) in 1996. During our field research, three adult females were captured at the control site in the West Usambara Mountains.

Ecology and Reproduction—Two females were captured in 1991 over a small stream flowing out of the WU control site. Both of these were found tangled in the net during the pre-dawn check and had large teats but were not lactating. The third specimen was captured in a furled bird net within the WU control site forest in 1993. This female had an open pubic symphysis and large teats but was not lactating. Both external (Table 2) and cranio-dental (Table 3) measurements fall within the range provided by Bergmans (1997) for this species.

Specimens Examined—**WEST USAMBARA**, 12.5 km NW Korogwe, Ambangulu Tea Estate, WU control site, 5 July 1991, 18 August 1993 (FMNH 147381, 147382, 151404).

Rousettus aegyptiacus (É. Geoffroy Sainte-Hilaire, 1810)

Distribution—*Rousettus aegyptiacus* is broadly distributed across Africa, particularly in coastal and lowland habitats, but largely unknown from montane settings within Tanzania (Bergmans, 1994; Stanley et al., 2005b, 2007a). Two geographically distinct subspecies have been recognized in sub-Saharan Africa (Bergmans, 1994), with *R. a. leachii* occurring in the eastern portion of this zone. This species was not captured during our surveys of the South Pare or West Usambara Mountains.

Ecology and Reproduction—In the East Usambara, five adults (four in 1992, one in 1993) were obtained, including two (one male in 1992 and one female in 1993) collected in a net set over a dam reservoir, one male at the edge of an open well cistern next to the 2.6-ha Bulwa fragment, and one female and one male over a stream in the ecotone between forest and tea plantation.

The three males collected in the first half of August 1992 were all scrotal. Two were dissected to assess reproductive status, of which one had testes measuring 15 by 10 mm and the other 17 by 12 mm, both with convoluted epididymides. The two captured females (collected in the first half of August in both 1992 and 1993) were pregnant—each carrying a single embryo, the largest with a crown–rump length of 7 mm.

Comments—Three males and two females were collected at sites in the East Usambara; the sample is too small to test for sexual dimorphism. However, based on the external and cranio-dental measurements presented by Bergmans (1994) and Kwiecinski and Griffiths (1999), females are smaller on average than males.

See the *Lissonycteris* account for characters to differentiate this genus from *Rousettus*. *Rousettus aegyptiacus* can be differentiated from *R. lanosus* by the presence of more rounded upper cheekteeth and very short, thin fur on the back. *Rousettus lanosus* has very narrow cheekteeth and thick fur.

Specimens Examined—**EAST USAMBARA**, 4.5 km WNW Amani, Monga Tea Estate, EU control site, 5 August 1992, 2 August 1993 (FMNH 150052, 151158); 4.5 km ESE Amani, Monga Tea Estate, EU control site, 14–16 August 1992 (FMNH 150054, 150408); 8 km NWN Amani, Bulwa Tea Estate, 12 August 1992 (FMNH 150053).

Rousettus lanosus Thomas 1906

Distribution—*Rousettus lanosus* is restricted to montane habitats in eastern and central Africa, including Democratic Republic of the Congo, Ethiopia, Kenya, Malawi, Uganda, and Tanzania (Bergmans, 1994; Simmons, 2005). Within Tanzania, this species has been documented on the mountains of Ngorongoro, Hanang, Kilimanjaro, West Usambara (at Isongo), Uluguru, and Mahenge (Bergmans, 1994). Based on the distribution of voucher material from montane zones in eastern Tanzania, Bergmans (1994) suggested that *R. lanosus* occurs in the "Para" range, which we assume is meant to be the Pares. No specimen of *R. lanosus* was collected during our surveys of the East or West Usambara Mountains, although Rodgers and Homewood (1982) list this species as occurring in the West Usambara.

Ecology and Reproduction—*Rousettus lanosus* was found in the South Pare Mountains and was the second most commonly captured bat at 1100 m (three males and 13 females) but was not found at 2000 m. Seven of the females captured between 19 and 24 July 1993 were examined for reproductive status and five were pregnant, all with single embryos—two with the embryos in the left uterine horn and three with the embryos in the right horn. The crown–rump length of the embryos was on average 17.8 mm (7.6, 7–27 mm; four of the

five individuals had embryos of 14 mm crown–rump length or greater); these measures are notably larger than the embryos for *L. angolensis* from the same site and period. Body weight differed considerably, reflecting the difference between pregnant and non-pregnant individuals (Table 2). All three males obtained in the South Pare Mountains had scrotal testes. The one specimen examined had testes measuring 10 by 5 mm with convoluted epididymides. External and cranio-dental measurements for each sex and field collector are presented in Tables 2 and 3.

Specimens Examined—**SOUTH PARE**, Chome Forest Reserve, 7 km S Bombo, 1100 m, 19–24 July 1993 (FMNH 151171–151178, 151405–151412).

Family Rhinolophidae
***Rhinolophus clivosus* Cretzschmar, 1828**

Distribution—*Rhinolophus clivosus* is widespread across the African continent from South Africa north to Egypt and then eastward to the Arabian Peninsula. Although mainly a savannah woodland species, it has been found at elevations up to 2300 m (Ansell & Dowsett, 1988) and is known from forest fringes. In Tanzania, this species has been documented from Kilimanjaro, Udzungwa, and Nguru Mountains (Csorba et al., 2003; W. T. Stanley, unpubl. data).

Ecology and Reproduction—In the East Usambara, five females and seven males were collected, of which nine were taken in intact montane forest and three in degraded forest mixed with *Maesopsis* trees. Most individuals were captured between 1830 and 1900 h. Of the four females examined, two (collected 17 August 1992) had small teats and two had large, non-lactating teats (collected during the first half of August in 1991 and 1993). Of the six males examined within the first half of August 1991, 1992, and 1993, three were scrotal and three had abdominal testes, one of which had testes that measured 4 by 3 mm with non-convoluted epididymides.

In the West Usambara, six females and nine males were collected. In 1991, two of these specimens were captured in bird nets placed within the control site in an area of largely primary forest, but with pockets of secondary habitat; the bats were netted in secondary habitat. Furthermore, two individuals were obtained in the 40-ha fragment forest, one in the 1.9-ha fragment, and another in a stand of *Eucalyptus* trees. In 1992, specimens were trapped in bird nets within the forest set at distances of 67.5 to 324 m to the edge. Two females were dissected: one was not in a reproductive state and the other had an embryo that measured 10 mm in crown–rump length. Four of the males collected between July and September 1991, 1992, and 1993 were scrotal, one of which measured 3 by 2 mm and had convoluted epididymides; the other five had abdominal testes.

In the South Pare Mountains, we caught three females and two males at 1100 m and one individual of each sex at 2000 m. The two males trapped at 1100 m had abdominal testes, but the male from 2000 m was partially scrotal. Two of three females collected at 1100 m had small teats; the third had large teats but was not lactating.

Comments—A one-way ANOVA test to assess levels of sexual dimorphism in external measurements in the East Usambara specimens revealed no significant differences. Among external measurements of West Usambara animals, weight was the only variable that differed significantly between the sexes, with females being heavier than males (female mean = 18.4, male mean = 15.5; F = 20.9, P = 0.001); this difference is associated with the additional weight of embryos in pregnant females.

Two of six females collected were examined for embryos; one was not pregnant (weight 15 g) and another had a single fetus that measured 10 mm in crown–rump length (weight 18.5 g). A one-way ANOVA to assess differences between the East and West Usambara samples (measured by S.M.G.) showed that *R. clivosus* from East Usambara had shorter hind feet and forearms than those from the West (Table 4). External measurements are presented for each field collector and mountain, but sexes are combined (Table 4).

Among cranio-dental characters, the three male animals from the West Usambara exhibited significantly longer length of the toothrow measured at the cingulum (LUTR) compared with two females (female mean = 8.3, male mean = 8.5; F = 28.1, P = 0.01). However, the same comparison for the three males and two females from the East Usambara showed no significant difference in this variable (female mean = 8.3, male mean = 8.3; F = 0.001, P = 0.97). When the samples from both mountains are combined and the sexes compared, there are no significant differences (female mean = 8.3, male mean = 8.4; F = 1.5, P = 0.25). Given the small sample sizes and that no other character exhibited sexual dimorphism, we do not attribute biological importance to this result. We combine the sexes and localities for the cranio-dental measurements in Table 5.

Rhinolophus clivosus has a high, rounded connecting process, and the first upper premolar is completely outside the toothrow. The rostral profile is nearly horizontal because of the reduced anterior median swellings (Csorba et al., 2003).

Specimens Examined—**EAST USAMBARA**, 4.5 km ESE Amani, Monga Tea Estate, EU control site, 17 August 1992, 7–8 August 1993 (FMNH 150071, 150410, 151192, 151419, 151420); 4.5 km WNW Amani, Monga Tea Estate, EU control site, 5–9 August 1991, 2–4 August 1992, 1 August 1993 (FMNH 147225, 147395–147397, 150066, 150070, 151418); **WEST USAMBARA**, 14.5 km NW Korogwe, Ambangulu Tea Estate, 20 July 1991 (FMNH 147392, 147393); 12.5 km NW Korogwe, Ambangulu Tea Estate, WU control site, 3–13 July 1991, 29 August–2 September 1992 (FMNH 147222, 147223, 147388–147391, 150068, 150069, 150411–150413); 11 km NW Korogwe, Ambangulu Tea Estate, 28–29 July 1991 (FMNH 147224, 147394); **SOUTH PARE**, Chome Forest Reserve, 7 km S Bombo, 1100 m, 18–20 July 1993 (FMNH 151193, 151194, 151423–151425); Chome Forest Reserve, 3 km E, 0.7 km N Mhero, 2000 m, 27 August 1994 (FMNH 153848, 153849).

***Rhinolophus deckenii* Peters, 1867**

Distribution—*Rhinolophus deckenii* is restricted to south-eastern Kenya, Uganda, eastern Tanzania (where collection localities include coastal forests and some Eastern Arc Mountains), and Mozambique (Monadjem et al., 2010). Stanley et al. (2005a) recorded *R. deckenii* from the Malundwe Mountains at 900 m in Mikumi National Park in dry submontane forest. This species was not captured in the South Pare or West Usambara Mountains.

Ecology and Reproduction—In the East Usambara, one scrotal male of *R. deckenii* was collected soon after dusk in slightly degraded montane forest in a bird net placed in the northeastern portion of the EU control site. Stanley et al. (2005a) found two color morphs in the Malundwe Mountains (cinnamon-brown and dull brown), as has been previously documented (Csorba et al., 2003). The specimen collected in the East Usambara was dull brown.

Comments—*Rhinolophus deckenii* has a wide horseshoe (>9 mm) and a semicircular connecting process, and the upper canine and posterior upper premolar are separated by a narrow gap (Csorba et al., 2003).

Specimen Examined—**EAST USAMBARA**, 4.5 km WNW Amani, Monga Tea Estate, EU control site, 5 August 1992 (FMNH 150409).

Rhinolophus fumigatus Rüppell, 1842

Distribution—*Rhinolophus fumigatus* is broadly distributed across sub-Saharan Africa. In Tanzania, this species has been collected mostly in the east, including both montane and coastal forest habitats. N. J. Cordiero captured one specimen in the Mgambo Forest Reserve of the East Usambara at 400 m in 1996 (FMNH 163396). Koopman (1994) recognized the form *R. f. exsul* Anderson, 1905, as occurring in Tanzania. This species was not trapped in the South Pare or West Usambara Mountains during our study.

Ecology and Reproduction—In the East Usambara, one female was obtained in August 1992 that had single embryos in each uterine horn, the largest of which was 4 mm in crown–rump length. Csorba et al. (2003) mentioned that this species is not found in forest habitat, but on the fringes, and Monadjem et al. (2010) considered it a savanna woodland species. Our East Usambara animal was netted at the edge of a dammed pond in an agricultural area. Other species captured in the same set and within one hour of the individual *R. fumigatus* include *Epomophorus wahlbergi*, *Neoromicia nanus*, *Pipistrellus hesperidus*, and *Scotophilus dinganii*.

Comments—*Rhinolophus fumigatus* has a wide horseshoe (>9 mm) and a low connecting process, and the upper canine and posterior upper premolar widely overlap each other (Csorba et al., 2003).

Specimen Examined—**EAST USAMBARA**, 8 km NWN Amani, Bulwa Tea Estate, 10 August 1992 (FMNH 150067).

Rhinolophus hildebrandti Peters, 1878

Distribution—*Rhinolophus hildebrandti* is distributed across eastern and southern Africa and is known from different localities in Tanzania, including the Udzungwa Mountains (Stanley et al., 2005b) and Gonja Forest Reserve at the base of the South Pare Mountains (Stanley et al., 2000). It was not collected on the South Pares or Tanzanian coastal forests at the base of the East Usambara Mountains (Stanley et al., 2005c).

Ecology and Reproduction—In the East Usambara Mountains, one male with abdominal testes was captured at the edge of the 2.6-ha Bulwa site near an open cistern, and two females were collected in August 1992 and 1993 near the village of Mbomole in a net set over a stream running through a marshy area. The reproductive condition of one of the two collected females was assessed, and it showed no sign of activity. In the West Usambara Mountains, one male was collected 15 July 1991 in partially cleared forest and had abdominal testes that measured 3 by 2 mm, with non-convoluted epididymides. Sexes are combined in presentation of external and cranio-dental measurements (Tables 4 and 5).

Comments—*Rhinolophus hildebrandti* is the largest known member of this genus in Tanzania, with a forearm length of greater than 60 mm and a horseshoe that is 12 mm or wider (Csorba et al., 2003).

Specimens Examined—**EAST USAMBARA**, 4.5 km WNW Amani, Monga Tea Estate, EU control site, 4 August 1992, 4 August 1993 (FMNH 150072, 151422); 8 km NWN Amani, Bulwa Tea Estate, 9 August 1992 (FMNH 150414); **WEST USAMBARA**, 12.5 km NW Korogwe, Ambangulu Tea Estate, WU control site, 15 July 1991 (FMNH 147226).

Rhinolophus simulator Anderson, 1904

Distribution—*Rhinolophus simulator* has a disjunct distribution across sub-Saharan Africa, with *R. s. simulator* to the east, from South Africa to Ethiopia, and *R. s. alticolus* in western Africa, from Cameroon to Guinea (Csorba et al., 2003; Monadjem et al., 2010). In Tanzania, the nominate form has been collected across broad elevational and habitat ranges, including Rukwa in the southwest and montane settings including Rubeho, Udzungwa (Kihansi Gorge), Uluguru, and Meru (Csorba et al., 2003; N. J. Cordeiro, unpubl. data; W. T. Stanley, unpubl. data). This species was not found in the East or West Usambara Mountains during our study.

Ecology and Reproduction—In the South Pare Mountains at the 2000-m site, one female was netted over a small stream deep within the forest. This individual had no embryo or placental scar, although the right oviduct was enlarged.

Comments—*Rhinolophus simulator* has a horseshoe that is less than 8.4 mm and a rounded, well-haired connecting process, and the first upper premolar is within the toothrow (Csorba et al., 2003).

Specimen Examined—**SOUTH PARE**, Chome Forest Reserve, 3 km E, 0.7 km N Mhero, 22 August 1994 (FMNH 153928).

Rhinolophus swinnyi Gough, 1908

Distribution—*Rhinolophus swinnyi* is known from the southern half of the African continent, but only a few localities in Tanzania, including the Udzungwa Mountains and Zanzibar (Kock & Howell, 1988). Although generally occurring in savanna woodland, some specimens have been collected in montane forests (Csorba et al., 2003).

Ecology and Reproduction—We only captured this species in the East Usambara Mountains, where two males and one female were collected. The female was netted adjacent to a water cistern next to the 2.6-ha Bulwa fragment and had no embryo or placental scar. One of the males was collected over a stream in the ecotone between forest and tea plantation, and the testes were partially scrotal. The other male was captured at the edge of a marsh next to the village of Mbomole and had abdominal testes.

Comments—The two male specimens were identified by the late Karl Koopman (pers. comm.) as *R. simulator*. However, we base our identification as *R. swinnyi* on characteristics listed by Csorba et al. (2003), namely narrow horseshoe and sella and short ear length.

Specimens Examined—**EAST USAMBARA**, 8 km NWN Amani, Bulwa Tea Estate, 11 August 1992 (FMNH 150073); 4.5 km WNW Amani, Monga Tea Estate, EU control site, 4 August 1993 (FMNH 151421); 4.5 km ESE Amani, Monga Tea Estate, EU control site, 14 August 1992 (FMNH 150415).

Family Nycteridae

Nycteris grandis Peters, 1865

Distribution—Both Van Cakenberghe and De Vree (1993) and Hickey and Dunlop (2000) indicate that *Nycteris grandis*

shows two disjunct populations: one in west central Africa (nominate *grandis*) and the other along the eastern half of Tanzania (the form *marica*). This species is generally a humid forest animal that can also be found in gallery forests, swampy areas, and woodland habitats (Hickey & Dunlop, 2000). Our surveys documented this species only in the East Usambara Mountains.

Ecology and Reproduction—One female was collected 2 August 1992, and two females were captured 30 and 31 July 1993 at the same site in the East Usambara. All three bats were captured in a mist net set on, or near, a bridge spanning a small stream in disturbed forest with some *Maesopsis* trees and a swampy area upstream. The one female for which the sexual organs were examined and obtained on 31 July had an embryo in the left uterine horn with a crown–rump length measuring 3 mm.

Comments—Kershaw (1923) described *N. marica* from Tindiga (Tendigo), Kilosa, Tanzania, based on the smaller skull dimensions and larger fourth lower premolar, as compared with typical *N. grandis*. Kock (1981) maintained that *marica* was a valid subspecies of *grandis* and that the form in eastern Africa was morphologically distinct from those in the western and central portions of the continent. However, Van Cakenberghe and De Vree (1993) found no support for the partition of *N. grandis* into subspecies. Our measurements of forearm length fall within the range given by Van Cakenberghe and De Vree (1993; Table 4). Monadjem et al. (2010) hypothesize that these two forms may represent different evolutionary lineages separated by habitat type.

Specimens Examined—**EAST USAMBARA**, 4.5 km WNW Amani, Monga Tea Estate, EU control site, 2 August 1992, 30–31 July 1993 (FMNH 150065, 151416, 151185).

147386); 11 km NW Korogwe, Ambangulu Tea Estate, 26–28 July 1991 (FMNH 147221, 147387).

Family Vespertilionidae

***Glauconycteris argentata* (Dobson, 1875)**

Distribution—*Glauconycteris argentata* has a broad distribution in the central portion of the African continent from Cameroon and Democratic Republic of the Congo eastward to Malawi and Kenya, with the southern-most record being Angola (Monadjem et al., 2010). In Tanzania, this species has been recorded from (north to south) near Gonja (at the base of the South Pare; Stanley et al., 2000) and at Kilosa, Morogoro, and Mwaya (on the northern tip of Lake Tanganyika; Swynnerton & Hayman, 1951).

Ecology and Reproduction—During the course of our inventories, two males were obtained in the East Usambara and one female in the West Usambara. In 1991, a female without signs of active reproduction, but large teats, was netted over a small stream at the edge of the WU control forest. In 1992, a male with abdominal testes measuring 2 by 1 mm and non-convoluted epididymides was captured over an open cistern next to the 2.6-ha Bulwa fragment, and in 1993, a male with abdominal testes was collected over a marshy area near Mbomole village. All specimens were adult, and due to the small sample size, sexes and localities are combined for presentation of external measurements in Table 4.

Specimens Examined—**EAST USAMBARA**, 4.5 km WNW Amani, Monga Tea Estate, EU control site, 4 August 1993 (FMNH 151428); 8 km NWN Amani, Bulwa Tea Estate, 11 August 1992 (FMNH 150074); **WEST USAMBARA**, 12.5 km NW Korogwe, Ambangulu Tea Estate, WU control site, 4 July 1991 (FMNH 147227).

***Nycteris thebaica* E. Geoffroy, 1818**

Distribution—*Nycteris thebaica* is broadly distributed from the Arabian Peninsula to South Africa. This species is found in a variety of habitats. Gray et al. (1999) state that it favors open woodland to moister forests, but Monadjem et al. (2010) maintain that quantifying the habitat preference of *N. thebaica* is difficult, although it appears to avoid open grasslands. In Tanzania, this species has been documented on the offshore islands of Mafia, Pemba, and Unguja and several localities on the mainland, including Amani in the East Usambara Mountains (Van Cakenberghe & De Vree, 1998). As currently recognized, *N. thebaica* occurs across a relatively broad elevational and habitat range.

Ecology and Reproduction—During our study, *N. thebaica* was only found in the West Usambara Mountains and only in the 1991 field season. One female was netted at sunset in a *Maesopsis* plantation; it had one embryo in the right uterine horn with a crown–rump length of 3 mm. Another female was found tangled in the thorns of a *Rubus* plant by its wing membranes, about 75 cm off the ground. This species, which is known to forage close to the ground and may even alight to capture invertebrate prey, has been captured in snap traps set on the ground (Kingdon, 1974; Stanley et al., 2005c, 2007b). One specimen was captured in a mist net at dusk in the 1.9-ha fragment next to a large tree with a hole at the base that led to a vertical hollow.

Specimens Examined—**WEST USAMBARA**, 14.5 km NW Korogwe, Ambangulu Tea Estate, 22 July 1991 (FMNH 147220,

***Myotis bocagei* (Peters, 1870)**

Distribution—*Myotis bocagei* is distributed throughout sub-Saharan Africa and known from Yemen (Simmons, 2005; Monadjem et al., 2010). Swynnerton and Hayman (1951) list this species from Kasanga, in the southern Udzungwa Mountains.

Ecology and Reproduction—One male was collected next to a pond near the Monga Tea factory in 1992. Its testes were abdominal and measured 5 by 3 mm, and the epididymides were not convoluted. Measurements of this single individual are presented in Tables 4 and 6.

Specimen Examined—**EAST USAMBARA**, 6 km NW Amani, Monga Tea Estate, 30 July 1992 (FMNH 150075).

***Scotophilus diuganii* (A. Smith, 1833)**

Distribution—*Scotophilus dinganii* is broadly distributed across sub-Saharan Africa (Simmons, 2005; Monadjem et al., 2010), although molecular data indicate that this species is paraphyletic or the individuals used in the study were misidentified (Trujillo et al., 2009). It has been recorded in Tanzania in habitats ranging from the coastal forests to inland savannah woodlands, such as Tarangire National Park (Robbins et al., 1985; Stanley et al., 2007c).

Ecology and Reproduction—All specimens (five females and two males) from the East and West Usambaras were collected in nets set over running or near standing water. For example, a female was trapped in 1991 over a small stream emerging from the forest of the WU control site, and the

TABLE 4. External measurements (mm) and weight (g) of microbats collected during the 1991–1994 surveys of the South Pare (SP), East Usambara (EU), and Western Usambara (WU) Mountains. Sexes are combined after a one-way ANOVA was conducted to test between sexes and mountain localities for more than three samples (see text). Measurements were taken by both S.M.G. and W.T.S.

	TL	HB	TV	HF	EAR	FA	WT
Rhinolophidae							
Rhinolophus clivosus S.M.G., EU, ♀, ♂							
Mean ± SD	106.0 ± 5.29		36.0 ± 3.19	10.1 ± 0.94	22.6 ± 0.81	54.2 ± 1.47	16.0 ± 1.08
Range	95–115		30–41	9–12	21–24	52–56	14.5–17.5
n	11		11	11	11	11	11
Rhinolophus clivosus W.T.S., EU, ♂	97	71	32	12	23	52	15.5
Rhinolophus clivosus S.M.G.,WU, ♀, ♂							
Mean ± SD	106.7 ± 5.58		36.8 ± 3.02	11.3 ± 1.36	22.8 ± 0.75	55.5 ± 1.17	16.7 ± 1.81
Range	95–115		32–41	9–14	22–24	53–57	14–20
n	12		12	12	12	12	12
Rhinolophus clivosus W.T.S., WU, ♀, ♂							
Mean ± SD	100.5 ± 4.95	74	30.5 ± 0.71	12.5 ± 0.71	21.5 ± 0.71	54.0 ± 0.00	14.8 ± 0.35
Range	97–104		30–31	12–13	21–22	54–54	14.5–15.0
n	2	1	2	2	2	2	2
Rhinolophus clivosus S.M.G., SP (1100 m), ♀, ♂							
Mean ± SD	107.8 ± 12.99		36.2 ± 3.27	9.4 ± 0.55	22.4 ± 0.55	56.2 ± 0.84	14.9 ± 1.34
Range	101–131		33–41	9–10	22–23	55–57	13–16
n	5		5	5	5	5	5
Rhinolophus clivosus W.T.S., SP (2000 m), ♀, ♂							
Mean ± SD	98.0 ± 1.41		30.0 ± 5.65	12.5 ± 0.71	21.5 ± 0.71	55.5 ± 0.71	14.8 ± 1.06
Range	97–99		26–34	12–13	21–22	55–56	14.0–15.5
n	2		2	2	2	2	2
Rhinolophus deckenii S.M.G., EU, ♂	102		37	10	24	57	14.5
Rhinolophus deckenii S.M.G., WU, ♂	109		37	11	24	56	16.5
Rhinoloplus fumigatus W.T.S., EU, ♀	98	70	30	13	25	56	17.5
Rhinolophus hildebrandti S.M.G., EU, ♀, ♂							
Mean ± SD	119.5 ± 7.78		39.0 ± 2.83	12.0 ± 1.41	34.5 ± 2.12	63.5 ± 3.53	23.5 ± 1.41
Range	114–125		37–41	11–13	33–36	61–66	22.5–24.5
n	2		2	2	2	2	2
Rhinolophus hildebrandti W.T.S., EU, ♀	119	79	38	12	35	62	25
Rhinolophus hildebrandti S.M.G., WU, ♂	122		38	15	38	63	23.5
Rhinolophus simulator W.T.S., SP (2000 m), ♀	73	52	23	9	18	44	6.6
Rhinolophus swinnyi W.T.S., SP, ♀	78		23	9	18	44	6.6
Rhinoloplus swinnyi S.M.G., EU, ♂							
Mean ± SD	75.0 ± 1.41		24.0 ± 1.41	6.5 ± 0.71	17.0 ± 0.00	43.5 ± 0.71	6.7 ± 0.78
Range	74–76		23–25	6–7	17–17	43–44	6.1–7.2
n	2		2	2	2	2	2
Rhinolophus swinnyi W.T.S., EU, ♂	73	52	23	9	18	44	6.6
Nycteridae							
Nycteris grandis S.M.G., EU, ♀							
Mean ± SD	154.0 ± 7.00		73.3 ± 1.53	13.0 ± 1.00	33.3 ± 0.58	62.3 ± 1.53	24.7 ± 0.58
Range	146–159		72–75	12–14	33–34	61–64	24–25
n	3		3	3	3	3	3
Nycteris thebaica S.M.G., WU, ♀							
Mean ± SD	109.3 ± 5.38		53.8 ± 2.75	10.0 ± 0.82	32.3 ± 2.06	43.3 ± 2.06	9.0 ± 1.35
Range	103–116		51–57	9–11	30–35	41–45	8–11
n	4		4	4	4	4	4
Vespertilionidae							
Glauconycteris argentata S.M.G., EU, WU, ♂, ♀							
Mean ± SD	104.0 ± 2.83		48.5 ± 0.71	6.0 ± 0.00	12.0 ± 1.41	42.0 ± 1.41	8.3 ± 0.35
Range	102–106		48–49	6–6	11–13	41–43	8–8.5
n	2		2	2	2	2	2
Glauconycteris argentata W.T.S., EU, ♂	96	56	44	8	12	41	7
Myotis bocagei W.T.S., EU, ♂	92		35	10	14	37	7.2

TABLE 4. *Continued.*

	TL	HB	TV	HF	EAR	FA	WT
Scotophilus dinganii S.M.G., EU, WU, ♀, ♂							
Mean ± SD	143.5 ± 2.74		59.0 ± 5.34	8.8 ± 1.17	17.7 ± 0.82	56.3 ± 1.03	24.8 ± 1.37
Range	140–148		49–65	8–11	17–19	55–57	24–27.5
n	6		6	6	6	6	6
Scotophilus dinganii W.T.S., WU, ♀	124	81	47	12	18	53	25
Scotophilus viridis S.M.G., EU, ♀, ♂							
Mean ± SD	128.5 ± 2.12		53.5 ± 3.54	10.0 ± 0.00	17.0 ± 0.00	51.5 ± 2.12	21.5 ± 2.83
Range	127–130		51–56	10–10	17–17	50–53	19.5–23.5
n	2		2	2	2	2	2
Pipistrellus hesperidus S.M.G., WU, ♀							
Mean ± SD	90.3 ± 2.96		38.2 ± 2.05	6.3 ± 0.50	11.6 ± 0.53	35.3 ± 0.50	5.7 ± 0.46
Range	87–95		36–42	6–7	11–12	35–36	5.1–6.5
n	9		9	9	9	9	9
Pipistrellus hesperidus S.M.G., EU, WU, ♂							
Mean ± SD	84.7 ± 4.27		37.1 ± 2.51	5.9 ± 0.34	11.0 ± 1.05	34.3 ± 0.67	5.5± 0.32
Range	78–91		32–40	5–6	10–13	33–35	5.0–6.0
n	10		10	10	10	10	10
Pipistrellus hesperidus W.T.S., WU, ♀	85	55	32	8	11	40	6
Pipistrellus hesperidus W.T.S., WU, ♂	85	55	33	7	11	34	4.8
Neoromicia nanus S.M.G., EU, SP, WU, ♀							
Mean ± SD	83.1 ± 1.45		36.2 ± 2.86	5.2 ± 0.67	10.3 ± 0.71	32.8 ± 0.67	3.3 ± 0.23
Range	81–86		34–42	4–6	9–11	32–34	3–3.6
n	9		9	9	9	9	9
Neoromicia nanus S.M.G., EU, SP, WU ♂							
Mean ± SD	80.5 ± 1.43		35.8 ± 2.97	4.8 ± 0.42	9.9 ± 0.88	31.7 ± 0.67	3.3 ± 0.15
Range	79–83		29–40	4–5	9–11	31–33	3–3.5
n	10		10	10	10	10	10
Neoromicia nanus W.T.S., WU, ♀							
Mean ± SD	88.0 ± 0.00	48.0 ± 1.41	36.5 ± 2.12	6.5 ± 0.71	11.5 ± 0.71	33.5 ± 0.71	3.4
Range	88–88	47–49	35–38	6–7	11–12	33–34	
n	2	2	2	2	2	2	1
Neoromicia nanus W.T.S., WU, ♂							
Mean ± SD	76.0 ± 1.41	42.5 ± 2.12	32.5 ± 0.71	6.0 ± 0.00	10.5 ± 0.71	30.5 ± 0.71	2.9 ± 0.14
Range	75–77	41–44	32–33	6–6	10–11	30–31	2.8–3.0
n	2	2	2	2	2	2	2
Miniopterus schreibersii S.M.G., EU, ♀, ♂							
Mean ± SD	104.5 ± 7.78		49.5 ± 3.54	6.8 ± 0.35	12.0 ± 0.00	43.5 ± 0.71	7.5
Range	99–110		47–52	6.5–7	12–12	43–44	
n	2		2	2	2	2	1
Miniopterus schreibersii W.T.S., EU, WU, ♀, ♂							
Mean ± SD	102.6 ± 7.57	57.4 ± 5.35	43.9 ± 6.44	9.3 ± 0.95	11.7 ± 0.76	42.7 ± 2.69	7.2 ± 0.80
Range	94–112	48–64	35–50	8.5–10	11–13	38–46	6.1–8.2
n	7	7	7	7	7	7	7

following year a male and female were netted at the same location. One of these males was examined and had abdominal testes that measured 3 by 2 mm with non-convoluted epididymides. In 1993, a female was captured at the same site. In 1992, one female with small teats and no embryos was netted next to a pond in an agricultural zone near Bulwa. Localities and sexes are combined in the external and craniodental measurements (Tables 4 and 6).

SPECIMENS EXAMINED—**EAST USAMBARA**, 8 km NWN Amani, Bulwa Tea Estate, 10 August 1992 (FMNH 150086); **WEST USAMBARA**, 12.5 km NW Korogwe, Ambangulu Tea Estate, WU control site, 3 July 1991, 1–2 September 1992, 22 August 1993 (FMNH 147235, 150087, 150088, 150421, 150422, 151453).

Scotophilus viridis (Peters, 1852)

DISTRIBUTION—Broadly distributed across sub-Saharan Africa (Simmons, 2005), including different portions of Tanzania (Robbins et al., 1985) and Pemba Island (W. T. Stanley, unpubl. data). Swynnerton and Hayman (1951) list this species from Morogoro, Tanzania. Based on a recent molecular analysis, this species appears to be paraphyletic, and the specific identity of the individuals used in that study need to be reexamined (Trujillo et al., 2009).

ECOLOGY AND REPRODUCTION—This species was only obtained in 1992 in the East Usambara Mountains. A male and a female were captured over a stream running through a small marsh below the village of Mbomole. Measurements of these two individuals are presented in Tables 4 and 6.

SPECIMENS EXAMINED—**EAST USAMBARA**, 4.5 km WNW Amani, Monga Tea Estate, EU control site, 4 August 1992 (FMNH 150084, 150085).

Pipistrellus hesperidus Temminck, 1840

DISTRIBUTION—Kock (2001) recently found *Pipistrellus herperidus* to be distinct from *P. kuhlii* (Kuhl, 1817). *Pipistrellus herperidus* is known from across the African

TABLE 5. Cranio-dental measurements of *Rhinolophus* from the East and West Usambaras. A one-way ANOVA found no significant differences between samples, so the mountains and sexes are combined.

Measurement	*Rhinolophus clivosus*	*Rhinolophus deckenii*	*Rhinolophus fumigatus*	*Rhinolophus hildebrandti*	*Rhinolophus swinnyi*
GLS					
Mean ± SD	22.5 ± 0.30	24.1	23.2	26.9 ± 0.10	17.8 ± 0.14
Range	22.0–23.0			26.9–27.0	17.7–18.0
n	11	1	1	3	3
CCL					
Mean ± SD	19.9 ± 0.27		20.7	24.0 ± 0.14	15.7 ± 0.08
Range	19.5–20.3			23.9–24.2	15.6–15.8
n	11		1	3	3
LUTR					
Mean ± SD	8.4 ± 0.14	9.2	8.8	9.6 ± 0.32	6.4 ± 0.09
Range	8.1–8.6			9.2–9.9	6.3–6.5
n	12	1	1	3	3
PAL					
Mean ± SD	2.3 ± 0.14	2.6	2.8	3.3 ± 0.33	2.0 ± 0.09
Range	2.1–2.6			2.9–3.5	1.9–2.1
n	12	1	1	3	3
MAST					
Mean ± SD	10.3 ± 0.21	10.8	10.9	12.2 ± 0.19	8.6 ± 0.02
Range	9.9–10.6			12.0–12.4	8.6–8.7
n	12	1	1	3	3
ZYG					
Mean ± SD	11.9 ± 0.24	12.0	12.6	14.0 ± 0.30	8.7 ± 0.07
Range	11.4–12.4			13.8–14.4	8.7–8.8
n	12	1	1	3	3
M^3-M^3					
Mean ± SD	8.6 ± 0.20	9.0	9.2	9.8 ± 0.31	6.2 ± 0.13
Range	8.3–8.9			9.4–10.1	6.0–6.3
n	12	1	1	3	3
ALSW					
Mean ± SD	5.9 ± 0.10	5.9	5.9	7.2 ± 0.23	4.6 ± 0.04
Range	5.7–6.1			7.0–7.5	4.6–4.7
n	12	1	1	3	3
AMSW					
Mean ± SD	3.6 ± 0.16	4.1	4.1	5.4 ± 0.04	3.0 ± 0.09
Range	3.3–3.9			5.4–5.4	2.9–3.0
n	12	1	1	3	3
IOW					
Mean ± SD	2.7 ± 0.18	2.6	2.6	2.8 ± 0.04	2.3 ± 0.03
Range	2.3–2.9			2.7–2.8	2.3–2.3
n	12	1	1	3	3
MAND con					
Mean ± SD	15.2 ± 0.31	16.6	16.1	18.7 ± 0.03	11.6 ± 0.08
Range	14.8–15.7			18.7–18.7	11.5–11.7
n	12	1	1	3	3
LLTR					
Mean ± SD	8.9 ± 0.18	9.8	9.4	10.4 ± 0.04	6.7 ± 0.17
Range	8.5–9.1			10.3–10.4	6.5–6.8
n	12	1	1	3	3
PAL/LUTR					
Mean ± SD	0.27 ± 0.02	0.28	0.32	0.34 ± 0.04	0.32 ± 0.01
Range	0.25–0.31			0.30–0.37	0.31–0.32
n	12	1	1	3	3

continent, the Canary Islands, and Madagascar (Bates et al., 2006; Monadjem et al., 2010). Further research based on voucher specimens and critical examination of holotypes may show that this taxon consists of several different species (Simmons, 2005). Within Tanzania, this species has been documented at Bagiro on the north slopes of the Uluguru Mountains (Swynnerton & Hayman, 1951). It was not recorded in the South Pare Mountains.

ECOLOGY AND REPRODUCTION—In the East Usambara, one male with abdominal testes was captured over a stream running through a small marsh below the village of Mbomole. In the West Usambara Mountains, we netted 10 females (three in 1991, six in 1992, and one in 1993) and 10 males (seven in 1991 and three in 1992) over a small stream issuing from the forest. Of the two females collected in early July 1991 and examined for reproductive condition, one was not pregnant and the other had

an embryo in each uterine horn, the largest measured 3 mm in crown–rump length. Three females collected 1 September 1992 were examined and showed no sign of active reproduction. All males collected had descended testes, which ranged from 4 to 7 mm in length by 3 to 4 mm in width.

Comparison of external measurements recorded by S.M.G. of the West Usambara sample indicated that females were significantly larger than males in total length ($F = 13.7$, $P = 0.002$), hind foot length ($F = 4.9$, $P = 0.04$), and forearm length ($F = 12.0$, $P = 0.003$). Tail length, ear length, and weight were not significantly different between the sexes. Descriptive statistics for this species are presented for each sex, with localities combined, because only two specimens were collected in the East Usambara Mountains (Tables 4 and 6).

Specimens Examined—**EAST USAMBARA**, 4.5 km WNW Amani, Monga Tea Estate, EU control site, 4 August 1992 (FMNH 150076); 8 km NWN Amani, Bulwa Tea Estate, 10 August 1992 (FMNH 150077); **WEST USAMBARA**, 12.5 km NW Korogwe, Ambangulu Tea Estate, WU control site, 3–5 July 1991, 1–4 September 1992, 22 August 1993 (FMNH 147229, 147231–147234, 147398–147402, 150080–150083, 150416–150420, 151435).

Neoromicia nanus (Peters, 1852)

Distribution—*Neoromicia nanus* is broadly distributed across sub-Saharan Africa (Monadjem et al., 2010). This species has been recorded across much of Tanzania, including Amani (Swynnerton & Hayman, 1951).

Ecology and Reproduction—*Neoromicia nanus* was found in all three mountain ranges surveyed during this study. In 1991, we captured two females over a small stream emerging from the forest of the West Usambara control site, neither showed signs of reproductive activity. In 1993, we netted two males, both with abdominal testes, and two females at the same location. In 1992, we caught three males, all near water, in the Bulwa area of the East Usambara Mountains, all of which had scrotal testes that measured 3 by 2 mm with non-convoluted epididymides. In 1993, one male was netted over a reservoir in disturbed forest on this massif.

In the South Pare Mountains, all specimens were collected at the 1100-m site in the second half of July 1993 and taken by local residents from the lower surfaces of banana leaves; the single exception was a female netted over the Mhokuvuta River. Seven specimens of each sex were collected. All males had at least partially descended testes, females collected by local residents were nulliparous, and the netted female was pregnant with an embryo in the left uterine horn measuring 6 mm in crown–rump length.

Specimens collected in the South Pare Mountains and measured by S.M.G. formed an adequate sample to examine patterns of sexual dimorphism in this taxon. Females were significantly larger than males in total length ($F = 16.1$, $P = 0.002$) and forearm length ($F = 10.6$, $P = 0.007$). Small sample sizes of each sex from the East and West Usambara Mountains prevented meaningful comparisons between localities. Descriptive statistics for external measurements are separated by sex and collector in Table 4.

Comments—Thorn et al. (2007) demonstrated the specific validity of *Vesperugo grandidieri*, which had long been synonymized with *N. capensis*, and they created a new genus for this species, *Afropipistrellus*. The samples used in this study came from forest reserves in the East Usambara Mountains, including Amani, Magroto, Longuza, Kwamgumi, Segoma, Kambai, and Nilo. We found no evidence of *V. grandidieri* in the vespertilionids collected during our 1991–1993 studies. The *Neoromicia* we collected have dark roots to the pelage and various cranial features, such as a narrow infraorbital constriction, braincase significantly elevated above the rostrum, and the "helmet" formed by the prominent sagittal and lambdoid sutures, characteristic of *N. nanus* (Rosevear, 1965).

Specimens Examined—**EAST USAMBARA**, 4.5 km WNW Amani, Monga Tea Estate, EU control site, 3 August 1993 (FMNH 151436); 8 km NWN Amani, Bulwa Tea Estate, 10 August 1992 (FMNH 150077–150079); **WEST USAMBARA**, 12.5 km NW Korogwe, Ambangulu Tea Estate, WU control site, 3 July 1991, 22 August 1993 (FMNH 147228, 147230, 151431–151434); **SOUTH PARE**, Chome Forest Reserve, 7 km S Bombo, 17–21 July 1993 (FMNH 151201, 151437–151449).

Family Miniopteridae
Miniopterus schreibersii (Kuhl, 1817)

Distribution—As currently defined, *Miniopterus schreibersii* is broadly distributed across southern Europe, Asia, Australia, and sub-Saharan Africa, but this taxon includes more than one species (Simmons, 2005; Furman et al., 2010). Recent molecular genetic work on this species complex demonstrated paraphyly between South African and Tanzanian individuals identified as *M. schreibersii* (Appleton et al., 2004). In Tanzania, *Miniopterus* attributed to this species have been collected in montane settings such as Mt. Kilimanjaro (W. T. Stanley, unpubl. data) and the Uluguru Mountains at Bagilo (Swynnerton & Hayman, 1951), as well as in the lowland forest at the base of the South Pare at Gonja (Stanley et al., 2000). Kingdon's (1974) map of this species range shows it occurring across eastern and southern Tanzania, but with no reference to specific locality names or voucher specimens. This species was not captured in the South Pare Mountains during our study.

Ecology and Reproduction—At the control site in the East Usambara Mountains, a male was netted in the ecotone between forest and tea plantation, and another male was captured above a small stream within the forest. In this same range, a female was obtained next to a pond in disturbed forest, and a second female was netted over a marshy area in the same forest. In the West Usambara control site, one female was trapped in 1992 and three females and one male in 1993, all over a small stream emerging from the forest. Of these individuals, the male had abdominal testes that measured 2 by 1 mm with non-convoluted epididymides, and the two examined females showed no sign of reproductive activity. Small sample sizes within each locality precluded critical testing for sexual or geographic differences in external and cranio-dental measurements (Tables 4 and 6).

Specimens Examined—**EAST USAMBARA**, 4.5 km WNW Amani, Monga Tea Estate, EU control site, 1–3 August 1993 (FMNH 151206, 151207); 4.5 km ESE Amani, Monga Tea Estate, EU control site, 17–23 August 1992 (FMNH 150089, 150091); **WEST USAMBARA**, 12.5 km NW Korogwe, Ambangulu Tea Estate, WU control site, 1 September 1992, 22 August 1993 (FMNH 150090, 151454–151457).

Discussion

Faunistics of the Three Studied Massifs

The surveys we conducted in the East and West Usambara and the South Pare Mountains were not specifically focused on bats, but rather were part of a large-scale project to

TABLE 6. Cranio-dental measurements of select vespertilionids and miniopterids from the East and West Usambaras. Mountains and sexes are combined.

Measurement	*Myotis bocagei*	*Scotophilus dinganii*	*Scotophilus viridis*	*Pipistrellus hesperidus*	*Neoromicia nanus*	*Miniopterus schreibersii*
GSKL						
Mean ± SD	15.5	22.0 ± 0.38	19.6 ± 0.31	13.0 ± 0.15	11.5 ± 0.25	14.8 ± 0.12
Range		21.4–22.5	19.4–19.8	12.7–13.2	11.2–11.8	14.7–15.0
n	1	6	2	11	4	5
CIL						
Mean ± SD	14.1	20.2 ± 0.44	18.6 ± 0.08	12.3 ± 0.19	10.9 ± 0.24	14.2 ± 0.15
Range		19.8–20.8	18.5–18.6	12.0–12.7	10.6–11.1	14.2–14.5
n	1	6	2	11	4	5
ZYG						
Mean ± SD	9.46	14.8 ± 0.15	13.4 ± 0.03	8.6 ± 0.09	7.0 ± 0.36	8.1 ± 0.05
Range		14.6–15.0	13.4–13.4	8.4–8.7	6.6–7.3	8.0–8.2
n	1	6	2	7	3	4
IOW						
Mean ± SD		4.8 ± 0.11	4.6 ± 0.20		3.2 ± 0.08	
Range		4.7–4.9	4.5–4.8		3.1–3.3	
n		6	2		4	
POW						
Mean ± SD	3.55			3.7 ± 0.10		3.6 ± 0.08
Range				3.6–3.9		3.6–3.7
n	1			11		5
MAST						
Mean ± SD	7.75	12.4 ± 0.30	11.3 ± 0.25		6.5 ± 0.21	8.1 ± 0.07
Range		12.1–12.8	11.2–11.5		6.2–6.8	8.1–8.2
n	1	6	2		4	5
BW						
Mean ± SD	7.5	9.8 ± 0.24	9.1 ± 0.04	6.5 ± 0.11	5.8 ± 0.17	7.5 ± 0.14
Range		9.3–10.0	9.0–9.1	6.4–6.7	5.6–6.0	7.3–7.6
n	1	6	2	11	4	5
PAL						
Mean ± SD	5.85	10.7 ± 0.35	9.9 ± 0.11		4.1 ± 0.08	5.4 ± 0.05
Range		10.2–11.1	9.8–9.9		4.0–4.2	5.3–5.5
n	1	6	2		4	5
LW						
Mean ± SD					4.0 ± 0.28	3.8 ± 0.04
Range					3.8–4.4	3.7–3.8
n					4	5
MAND con						
Mean ± SD	11.1	15.2 ± 0.68	14.1 ± 0.17	9.0 ± 0.20	7.5 ± 0.16	10.6 ± 0.12
Range		14.4–16.1	13.9–14.2	8.6–9.3	7.3–7.7	10.5–10.7
n	1	6	2	11	4	5
I^1-M^3						
Mean ± SD	6.54					6.6 ± 0.05
Range						6.5–6.6
n	1					5
C^1-M^3						
Mean ± SD	5.44	7.1 ± 0.14	6.6 ± 0.01	4.7 ± 0.10	3.9 ± 0.17	5.5 ± 0.03
Range		7.0–7.8	6.6–6.6	4.5–4.9	3.7–4.0	5.5–5.6
n	1	6	2	11	4	5
C^1-C^1						
Mean ± SD	3.95	7.4 ± 0.24	6.5 ± 0.20	4.1 ± 0.13	3.4 ± 0.12	4.0 ± 0.05
Range		7.1–7.8	6.4–6.6	4.0–4.4	3.2–3.5	3.9–4.1
n	1	6	2	10	4	5
M^3-M^3						
Mean ± SD	5.93	9.4 ± 0.19	8.4 ± 0.05		4.6 ± 0.20	5.8 ± 0.04
Range		9.2–9.7	8.3–8.4		4.3–4.8	5.8–5.9
n	1	6	2		4	5
UPMOLS						
Mean ± SD	4.71					4.6 ± 0.06
Range						4.5–4.7
n	1					5

TABLE 6. *Continued.*

Measurement	*Myotis bocagei*	*Scotophilus dinganii*	*Scotophilus viridis*	*Pipistrellus hesperidus*	*Neoromicia nanus*	*Miniopterus schreibersii*
I_1-M_3						
Mean ± SD	7	8.9 ± 0.13	8.1 ± 0.27	5.0 ± 0.12		6.9 ± 0.09
Range		8.7–9.1	7.9–8.3	4.8–5.2		6.8–7.1
n	1	6	2	11		5
lowermols						
Mean ± SD	5.18					5.3 ± 0.05
Range						5.3–5.4
n	1					5

inventory small terrestrial mammals. Hence, the bat captures were largely opportunistic, and the resulting species lists and measures of species richness should be considered preliminary. Species diversity across these mountains (Table 1) differs with the highest number from the East Usambara (n = 16), followed by the West Usambara (n = 11), and then the South Pare (n = 5). This variation might reflect patterns of species richness, but our measures are closely associated with sampling effort (see below).

Species common to all three massifs include two pteropodids (*Epomophorus wahlbergi* and *Lissonycteris angolensis*), one *Rhinolophus* (*R. clivosus*), and one vespertilionid (*Neoromicia capensis*). Of the 20 species documented during our bat surveys on these three mountains, taxa only found on a single massif include: *Rousettus lanosus* and *Rhinolophus simulator* (South Pare, 10% of total); *Myonycteris relicta* and *Nycteris thebaica* (West Usambara, 10% of total); and *Rousettus aegyptiacus, Rhinolophus deckenii, R. fumigatus, R. swinnyi, N. grandis, Myotis bocagei*, and *Scotophilus viridis* (East Usambara, 35% of total).

Sampling effort may explain some of these differences in species richness among the massifs. Mist nets set specifically for bats were in place in the South Pare for a total of 12 nights (eight at 1100 m and four at 2000 m), in the West Usambara for a total of 20 nights (11 in 1991, seven in 1992, two in 1993), and in the East Usambara for a total of 27 nights (three in 1991, 16 in 1992, eight in 1993). Furthermore, incidental trapping effort took place in the East and West Usambara Mountains associated with bird nets set for W. D. Newmark's study of understory birds. Bats found in the bird nets, all within forest, include *Epomophorus wahlbergi, Lissonycteris angolensis, Myonycteris relicta, Rhinolophus clivosus*, and *R. deckenii*; these species were also captured in nets we set specifically for bats.

Other Species of Bats Recorded in the Usambara Mountains and Nearby Regions

Comparing taxa previously reported from these massifs to those we collected can evaluate the effectiveness of bat inventories of the Usambaras (Table 7). An important caveat is that many taxa cited in the literature are not necessarily based on voucher specimens from which identifications can be properly verified.

A number of other taxa with verifiable voucher specimens add information regarding the regional fauna. Particularly interesting in this regard is a number of species that have been documented in the Usambaras outside of our inventories, which include the synanthropic occurrence of *Chaerephon pumilus* (Cretzschmar, 1830–1831) at Amani and the holotype of *Otomops martiensseni* (Matschie, 1897), a species poorly represented among collections of Tanzanian bats (Table 7). With the addition of these other records, 46 species are cited from the East Usambara, 28 of which were not recorded during our inventories of this massif.

Numerous other species are recorded to the east—specifically, between the foot of the East Usambara and Tanga along the coast, including *Hipposideros cyclops* (Temminck, 1853) from the Kwamgumi Forest Reserve (Stanley et al., 2005c), and *Triaenops persicus* Dobson, 1871, *Coleura afra* (Peters, 1852), and *Miniopterus minor* Peters 1867 from the Amboni Caves (Weyeneth et al., 2008; W. T. Stanley, unpubl. data).

Of the species listed in Table 7, certain ones, particularly some of those without associated voucher specimens, appear to be anomalous. For example, the eastern edge of the distribution of *Scotophilus nucella* Robbins, 1973, is thought to be Uganda, and other than the dubious records cited in Table 7 of *Neoromicia flavescens* (Seabra, 1900), this species is not known from Tanzania (Simmons, 2005) and is a nomen dubium (Thorn et al., 2007). *Epomophorus anurus* Heuglin, 1864, is a synonym of *E. labiatus* (Temminck, 1837), and the recorded distribution of this taxon within Tanzania is in the northwest (Bergmans, 1988).

Comparisons to Other Regional Sites

The diversity of species documented during this study in montane habitats of three Eastern Arc Mountains results from three years (two months each year) of occasional and opportunistic sampling. These limited efforts collected fewer species than known in lowland zones or habitats at the same general elevation but with different forest type in western Tanzania (Table 8). The two sites we use in these comparisons are Gonja Forest Reserve at 500 m at the base of the South Pare Mountains (Stanley et al., 2000) and Minziro Forest at 1150 m in northwestern Tanzania (Stanley & Foley, 2008).

Comparison of sampling effort (net hours), number of individuals, and number of species are presented in Table 8. We stress that these comparisons are rough because nets used at many of the montane sites were left in place for the entire night unmonitored, and some bats undoubtedly escaped. Additionally, the question of net placement at each site needs to be taken into account. For example, the stream that the Gonja net spanned may have been the only water source for some distance, and bats came to drink or catch insects. Nonetheless, species diversity and net trap success generally increase at both Gonja and Minziro, compared with the montane sites. In the Gonja dry forest, Stanley et al. (2000) caught 27 bats representing 11 species using one 12-m net for 2.5 h per night for six nights (12.5 net hours). Of these 11 species, eight were documented during our study of the

TABLE 7. Different bat species reported in the Usambara Mountains and surrounding areas but not recorded during our surveys of the regional montane forests. Specific details on the different localities are presented at the foot of the table.

Species	Locality[1]	Reference
Epomophorus anurus	10	Frontier-Tanzania
Rousettus lanosus	2	Frontier-Tanzania
Rhinolophus eloquens	1, 2, 3, 8, 9, 10	Frontier-Tanzania
Rhinolophus landeri	2, 7, 10, 12, 14, 16	Frontier-Tanzania
Rhinolophus maendeleo	4	Kock et al. (2000)
Hipposideros caffer	2, 3, 7, 15	Frontier-Tanzania
Hipposideros cyclops	13, 14	Frontier-Tanzania
Hipposideros ruber	2, 3, 7, 10, 11, 12, 14, 15	Frontier-Tanzania
Triaenops persicus	1, 2, 7, 10, 11, 12, 14	Frontier-Tanzania
Taphozous mauritianus	11	Frontier-Tanzania
Nycteris hispida	3, 11	Frontier-Tanzania
Nycteris macrotis	3, 8	Frontier-Tanzania
Chaerephon ansorgei	11	Frontier-Tanzania
Chaerephon pumilus	1, 5	Frontier-Tanzania, Aspetsberger et al. (2003)
Otomops martiensseni	6	Specimens in FMNH
Mops brachyptera	1, 9, 11, 12	Frontier-Tanzania
Nycticeinops schlieffeni[2]	16	Frontier-Tanzania
Scotophilus nucella	3, 10, 11	Frontier-Tanzania
Vesperugo grandidieri[3]	1, 2, 3, 5, 7, 9, 10, 11, 13, 14	Thorn et al. (2007), Frontier-Tanzania
Neoromicia flavescens[4]	3, 9, 11, 13	Frontier-Tanzania
Neoromicia rendalli[5]	10	Frontier-Tanzania
Scotoecus hindei	11	Frontier-Tanzania
Scotoecus hirundo	1, 8, 11	Frontier-Tanzania
Mimetillus moloneyi	1	Frontier-Tanzania
Miniopterus fraterculus	2, 10, 12	Frontier-Tanzania
Miniopterus minor	3, 7	Frontier-Tanzania
Kerivoula argentata	3, 7	Frontier-Tanzania

[1] Details on different localities: (1) Tanzania, Tanga Region, Muheza District, Magoroto Oil Palm Estate, 38°45′E, 5°7′S, 650–770 m (Cunneyworth et al., 1996b). (2) Tanzania, Tanga Region, Muheza District, Amani Nature Reserve, 38°30′34″–38°40′6″E, 5°14′10″–5°4′30″S, 190–1130 m (Doody et al., 2001b). (3) Tanzania, Tanga Region, Muheza District, Kambai Forest Reserve, 38°42′E, 5°0′S, 220–590 m (Cunneyworth et al., 1997b). (4) Tanzania, Tanga Region, Lushoto District, West Usambara Mountains, Mazumbai Forest Reserve, 38°15′E, 4°25′S, 1400–1900 m (Kock et al., 2000). (5) Amani (Thorn et al., 2007). (6) Magrotto Plantation, west of Tanga, southeastern Usambara Mountains (FMNH specimens). (7) Tanzania, Tanga Region, Muheza District, Bamba Ridge Forest Reserve, 38°47′E, 4°58′S, 150–1033 m (Cunneyworth et al., 1996c). (8) Tanzania, Tanga Region, Muheza District, Kwamarimba Forest Reserve, 38°45′E, 5°2′S, 95–445 m (Cunneyworth et al., 1996a). (9) Tanzania, Tanga Region, Muheza District, Longuza North Forest Reserve, 38°41′E, 5°2′S, 95–345 m (Cunneyworth et al., 1997a). (10) Tanzania, Tanga Region, Muheza District, Mtai Forest Reserve, 38°44′–38°48′E, 4°51′–4°54′S, 180–1016 m (Doggart et al., 1999b). (11) Tanzania, Tanga Region, Muheza District, Kwamgumi Forest Reserve, 38°44′–38°47′E, 4°55′–4°57′S, 150–915 m (Doggart et al., 1999a). (12) Tanzania, Tanga Region, Muheza District, Manga Forest Reserve, 38°45′–38°47′E, 5°0′–5°2′S, 120–360 m (Doggart et al., 1999c). (13) Tanzania, Tanga Region, Muheza District, Segoma Forest Reserve, 38°43′–38°47′E, 4°57′–5°1′S, 80–920 m (Doody et al., 2001a). (14) Tanzania, Tanga Region, Korogwe and Muheza Districts, Nilo Forest Reserve, 38°37′–38°41′E, 4°50′–4°59′S, 400–1506 m (Beharrell et al., 2002). (15) Tanzania, Tanga Region, Muheza District, Mlinga Forest Reserve, 38°44′–38°46′E, 5°4′–5°5′S, 220–1069 m (Hall et al., 2002). (16) Tanzania, Tanga Region, Muheza District, Mgambo Forest Reserve, 38°47′–38°49′E, 4°44′–4°47′S, 320–820 m (Oliver et al., 2002).

[2] Identified as *Nycticeius schlieffeni.*

[3] Identified as *Pipistrellus g. grandidieri.*

[4] Identified as *Pipistrellus flavescens* or *Eptesicus flavescens.*

[5] Identified as *Eptesicus rendalli.*

TABLE 8. Sampling effort and resulting numbers of individuals and species caught for three Eastern Arc Mountains, Gonja Forest Reserve, a dry lowland forest, and Minziro Forest Reserve, a Guinea-Congo forest in western Tanzania. Sites marked with an asterisk (*) represent efforts that included nets left operational the entire night. Sites not marked with an asterisk represent efforts in which the net was opened for only two to three hours at a time.

Site	Elevation (m)	Year	Net hours	No. of individuals	No. of species
East Usambara*	900–1150	1992	132	17	7
East Usambara*	900–1150	1993	18	8	5
West Usambara*	1150–1300	1991	96	25	4
West Usambara*	1150–1300	1992	24	13	4
West Usambara*	1150–1300	1993	24	10	5
South Pare*	1100	1993	12	23	2
South Pare	2000	1994	4	5	3
Gonja	500	1993	12.5	27	11
Minziro	1050	2006	8	58	9

montane bat fauna of the East Usambara, West Usambara, and South Pare Mountains. The three species only found at Gonja are *Hipposideros caffer* (Sundevall, 1846), *Nycteris hispida* (Schreber, 1775), and *Scotoecus hirundo* (de Winton, 1899). At the 1100-m site in the South Pare Mountains, approximately 8 km away from Gonja, 12 net hours were accrued with a single net, and 23 individuals were captured, representing only two species.

In the Minziro Forest at 1150 m, which consists of a Guinea-Congo forest, a single net was in place at the edge of a pond for four consecutive nights, each night for two hours (1800–2000 hrs), accruing eight net hours, and 58 bats were captured of nine species (Stanley & Foley, 2008). Only two of these, *Nycteris grandis* and *Neoromicia nanus*, were captured at the three Eastern Arc Mountain sites reported herein. Results from efforts conducted at a similar elevation in the East Usambara (separated by year), show notably fewer captures and slightly lower species diversity (Table 8). Thus, although these comparisons are preliminary, the bat fauna of the montane localities of the South Pare and East and West Usambara Mountains documented during our study appears to be less rich than other sites in Tanzania.

To have a more comprehensive view of the bat fauna of the Usambara and South Pare Mountains, more systematic bat surveys are needed, covering a greater range of elevations and variety of habitats than during our preliminary work. These data will be important for providing more detailed information, which will provide further insights into the faunistics and biogeography of the regional bat fauna.

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Chapter 4

Small Mammal Inventories in the East and West Usambara Mountains, Tanzania. 4. Rodentia

William T. Stanley[1] and Steven M. Goodman[1]

[1]*Department of Zoology, Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, IL 60605, USA*

Abstract

During three field seasons between 1991 and 1993, we carried out rodent inventories of the East and West Usambara Mountains, Tanzania. The general trapping protocol used involved both pitfall lines and trap lines (Sherman, Victor, and Museum Special traps), with a limited number of animals trapped within and outside of forest habitats by local people. A total of 885 individual rodents, representing 15 species, were collected during this study. For the East and West Usambara Mountains, 13 (12 native) and 12 (all native) rodent species were recorded, respectively. Most rodents were captured by trap lines (96.6%); a few individuals were captured in the pitfall devices or brought to us by local people. The major exception is that all individuals of *Dendromus* (n = 11) obtained during the survey were in pitfall buckets.

A total of 18,563 sample-nights were accrued over the three years, including 11,339 sample-nights (3314 pitfall-nights and 8025 trap-nights) in the East Usambara and 7224 sample-nights (1924 pitfall-nights and 5300 trap-nights) in the West Usambara Mountains. Based on species accumulation curves, no previously unrecorded species was trapped after 11,064 sample-nights in the East Usambara and after 5213 sample-nights in the West Usambara. However, a previously untrapped rodent (*Graphiurus kelleni*) was captured in the East Usambara on the third-to-last of 59 sampling days, suggesting that other non-canopy–restricted rodent species may have been missed during this survey. In a series of species accounts, information regarding the natural history of the different taxa handled during these surveys, including distribution, ecology, and condition of sexual organs, a list of referable specimens, and the trap devices that collected them, are presented.

Trap and bucket lines combine to effectively sample most small- to medium-sized rodents. However, larger scansorial and canopy-restricted (squirrel) and fossorial (mole rat) species were not captured with our trapping methods, and these tabulations should not be considered a complete list of the small mammals of the Usambaras.

Introduction

The montane forests of Tanzania contain diverse faunal assemblages, many of which have high levels of endemism. Some vertebrate taxa in these forests, such as amphibians, birds, and reptiles, have been studied by multiple generations of field researchers (e.g., Barbour & Loveridge, 1928; Loveridge, 1935, 1937; Moreau, 1935; Stuart, 1983; Newmark, 1991, 2002, 2006; Gravlund, 2002; Bowie et al., 2004; Menegon et al., 2008; Blackburn & Measey, 2009; Newmark et al., 2010). However, mammals, specifically the smaller species, have received notably less attention. Although there have been previous investigations of Tanzanian montane forest shrews (Hutterer, 1986; Stanley & Olson, 2005), bats (Kock & Howell, 1988; Kock et al., 2000), and rodents (Makundi et al., 2003, 2006; Carleton & Stanley, 2005), the past two decades have seen first-time small mammal surveys on mountains across the country (e.g., Stanley et al., 1996, 1998a, 2007a,b; Stanley & Hutterer, 2007; Mulungu et al., 2008). Over the course of three field seasons between 1991 and 1993, we carried out field inventories of the small mammals of the East and West Usambara Mountains, which are part of the Eastern Arc Mountains. Here, we present the results of these rodent surveys, whereas those pertaining to shrews and bats are reported in Stanley et al. (this volume a) and Stanley and Goodman (this volume), respectively.

Several different studies have been conducted on the rodents of Tanzania in lowland areas associated with their role in diseases that affect humans or as crop pests (e.g., Leirs et al., 1997; Mwanjabe & Leirs, 1997; Makundi et al., 2008). The importance of commensal rodents and their ectoparasites as reservoirs of plague has generated considerable research in montane areas, particularly in the West Usambara Mountains (e.g., Makundi, 1995; Kilonzo et al., 1997).

Based on preliminary inventories, Rodgers and Homewood (1982) listed known mammal species, including rodents, from the East and West Usambara Mountains. Subsequently, through a series of field inventories on different massifs, there has been a focus on the rodent faunas of relatively intact montane habitats across the Eastern Arc Mountains (Stanley et al., 1998a,b, 2007a,b; Stanley & Hutterer, 2007), based on surveys of up to two months. The current study compiles data on East and West Usambara rodents living in several different natural and anthropogenic habitats, including monotypic

TABLE 1. Rodent species and number of individuals captured in traps or pitfall lines in three seasons of faunal surveys of the East and West Usambara Mountains between 1991 and 1993 based on accrued sample nights.

Mountain range	East Usambara				West Usambara				Totals
	1991	1992	1993	EU Total	1991	1992	1993	WU Total	
Accrued number of sample nights	476	8252	2611	11,339	5213	1512	499	7224	18,563
Species									
Dendromus mystacalis	0	11	0	11	0	0	0	0	11
Beamys hindei	0	6	2	8	1	0	0	1	9
Lophuromys aquilus	8	91	19	118	42	8	2	52	170
Aethomys hindei	0	0	0	0	1	0	0	1	1
Grammomys ibeanus	0	3	0	3	19	1	2	22	25
Grammomys macmillani	0	10	1	11	11	0	0	11	22
Hylomyscus arcimontensis	5	31	9	45	93	43	5	141	186
Mastomys natalensis	0	1	0	1	7	0	0	7	8
Mus minutoides	0	1	0	1	1	0	0	1	2
Praomys delectorum	6	186	54	246	80	66	18	164	410
Rattus rattus[1]	0	4	0	4	0	0	0	0	4
Graphiurus kelleni	0	0	1	1	0	0	0	0	1
Graphiurus murinus	0	4	0	4	15	3	0	18	22
Total no. of individuals	19	348	86	453	270	121	27	418	871
Total no. of species	3	10	6	12	10	5	4	10	13
Trap success for rodents (%)	4.0	4.2	3.3	4.0	5.2	8.0	5.4	5.8	4.7

[1] Non-native species.

plantations of tea (*Camellia sinensis*) and *Eucalyptus*, fallow and recently tilled agricultural land, and native montane forest.

Study Area

Stanley et al. (this volume b) detail the specific study sites and the dates of the field inventories. Rodents were sampled from forested and agricultural sites on the Bulwa, Kwamkoro, and Monga Tea estates in the East Usambara and the Ambangulu Tea Estate in the West Usambara between 1991 and 1993 (see Stanley et al., 2011b, figs. 3–5).

Materials and Methods

The general trapping protocol used during this study involved both pitfall lines and trap lines; Stanley et al. (this volume b) report the specific details on these techniques. Although some rodents were captured in pitfall buckets, these were relatively limited and tended to be small species or juveniles of larger taxa. Given that each trap was checked in the early morning and again in the mid-afternoon (while adding fresh bait), the period that an animal was captured, hence activity period, could be ascertained as to between dusk and dawn or between dawn and dusk. A "bucket-night" or "trap-night" refers to one bucket or one trap in operation for a 24-h period (0700–0700 h), and the term "sample-night" is used in discussion of overall sampling effort (the combined number of bucket-nights and trap-nights). In a few cases, people living in vicinity of the study sites trapped various rodents within and outside of forest habitats and offered these animals to us.

We follow the species definitions of Holden (2005) for the Gliridae, Musser and Carleton (2005) for the Muridae and Nesomyidae, Thorington and Hoffman (2005) for the Sciuridae, and Woods and Kilpatrick (2005) for the Bathyergidae. Field Museum of Natural History (FMNH) catalog numbers are presented for cited vouchers in each species account. Details are also given on the trapping method for each captured animal; specific placement of the pitfall lines (PF) and trap lines (TRL) are presented in Stanley et al. (this volume b).

External measurements accurate to 1 mm were recorded for each specimen by one of the two field collectors (S.M.G. and W.T.S.), and definitions of these measures and their acronyms are presented in Stanley et al. (this volume a). Adult rodents are defined as having a fully erupted third upper molar and completely fused suture between the basioccipital and basisphenoid bones. When describing aspects of the reproductive state of males, testes are described as either abdominal or scrotal and measurements are presented in millimeters as length by width. The epididymis is referred to as either convoluted or not convoluted.

Results

A total of 1311 mammal specimens was collected during this three-year study, including 885 individual rodents representing 15 species. For the East and West Usambara Mountains, 13 (12 native) and 12 (all native) rodent species were recorded, respectively. Most captured rodents (96.6%) were from the trap lines; a few were captured in the pitfall devices (notably, all individuals of *Dendromus* [n = 11] obtained during the survey) or brought to us by local people. A total of 17,692 sample-nights were accrued over the three years, including 11,081 sample-nights (3314 pitfall-nights and 7767 trap-nights) in the East Usambara and 6611 sample-nights (1936 pitfall-nights and 4675 trap-nights) in the West Usambara (Table 1).

In the context of our trap and pitfall efforts (excluding specimens caught by hand), 1132 specimens were collected,

representing 13 rodent species. The East Usambara yielded 12 species of rodent and the West Usambara 10 species of rodent. As demonstrated previously for montane areas of east Africa (Stanley et al., 1996, 1998a,b), trap and bucket lines combine to sample the shrew and small- to medium-sized rodent faunas of a given area effectively.

Stanley et al. (this volume b) presents species accumulation curves separately across the three-year study (1991–1993) for the East and West Usambaras. No previously unrecorded species was trapped after 10,804 sample-nights in the East Usambara (where sample-nights totaled 11,081) and after 4600 sample-nights in the West Usambara (where sample-nights totaled 6611). The final previously untrapped rodent species obtained in the East Usambara was *Graphiurus kelleni,* which was captured on the third-to-last of 59 sampling days, suggesting that other non-canopy–restricted rodent species may have been missed during this survey.

Accounts of Species

Fifteen rodent species were documented for the East and West Usambara Mountains combined during the three-year study. External measurements are presented in Tables 2 and 3. In the following accounts, information for each species regarding their natural history (including distribution, ecology and reproduction), specimens examined (including museum catalog numbers and identifying pitfall lines [PF] and trap lines [TRL] where each specimen was collected [see Stanley et al., this volume b]), and, when necessary, other remarks are presented.

Family Sciuridae
Paraxerus vexillarius (Kershaw, 1923)

Distribution—The type locality of *Paraxerus vexillarius* is Lushoto, West Usambara (Kershaw, 1923). Kingdon (1974a, 1997) states that this species is only known from this massif. However, specimens referable to *P. vexillarius* have been collected in the Nguru, Rubeho, Udzungwa, Ukinga, and Uluguru Mountains (in FMNH). The Usambara specimens exhibit the orange feet and tail tip characteristic of the species (Kingdon, 1974a).

Ecology and Reproduction—Three female *P. vexillarius* were captured by hunters using dogs and brought to our camp on 21 July 1991. The reproductive tracts of two specimens were examined: One was nulliparous and the other had one placental scar in the left uterine horn. External measurements are presented in Table 2.

Specimens Examined—**WEST USAMBARA**, 12.5 km NW Korogwe, Ambangulu Tea Estate (captured by hand—FMNH 147236, 147237, 147403).

Family Nesomyidae: Subfamily Dendromurinae
Dendromus mystacalis (Heuglin, 1863)

Distribution—This species is distributed across central and eastern Africa, from southern Sudan to Angola and eastern South Africa (Musser & Carleton, 2005). Within Tanzania, specimens have been collected in various habitats, including dry woodland areas (e.g., Tarangire National Park [Stanley et al., 2007c]), and zones of higher elevation from western Tanzania, such as the Mahale Mountains (W. T. Stanley, unpubl. data) to the East Usambara.

Ecology and Reproduction—We trapped eight males and three females in 1992 but none in 1991 or 1993. The testes positions in five males were scrotal and in the other three abdominal. The mean testis measurement in six dissected specimens was 5.3 by 3.2 mm, and all but one individual had convoluted epididymides. Of the two females examined, one had large teats and the other small.

All *Dendromus* were captured by pitfall lines installed in tea plantations. Pitfall line 16 was the most productive for this species, especially near the middle of the line, catching nine of the 11 individuals (82%) collected. *Dendromus* was the most common mammal we captured in tea plantation habitat. External measurements are presented in Table 2.

Comments—Musser and Carleton (2005) suggest that this species as currently configured may contain more than one species. The holotype was collected in Ethiopia, a considerable distance from the Eastern Arc Mountains. Specimens collected during this study were identified by the fifth hind toe having a claw (as opposed to a nail) and greatest length of the skull less than 22 mm (Misonne, 1974).

Specimens Examined—**EAST USAMBARA**, 4.5 km WNW Amani, Monga Tea Estate, control site (PF 29—FMNH 150098); 6 km NW Amani, Monga Tea Estate (PF 16—FMNH 150092–150097, 150424–150426; PF 24—FMNH 150427).

Family Nesomyidae: Subfamily Cricetomyinae
Beamys hindei (Thomas, 1909)

Distribution—The genus *Beamys* is known to occur from southeastern Kenya to the eastern half of Tanzania and south into Malawi and Zambia (Musser & Carleton, 2005). Within Tanzania, *B. hindei,* as currently defined, has been recorded in lowland coastal forests and montane areas (Christensen, 1987; Fitzgibbon et al., 1995; Stanley et al., 1998a,b). We have recorded it in the following montane areas within Tanzania (north to south): South Pare, West Usambara, East Usambara, Ukaguru, Nguu, Nguru, Malundwe, Rubeho, Udzungwa, and Rungwe Mountains (Stanley et al., 1998a,b; Stanley & Hutterer, 2007; W. T. Stanley, unpubl. data).

Ecology and Reproduction—In the East Usambara, seven of eight specimens collected were taken in the control site in either undisturbed or only slightly disturbed forest. The single exception was an individual in the 0.2B-ha fragment, an isolated block of heavily disturbed forest. Specimens were obtained in terrestrial or arboreal trap sets, reflecting mixed substrate use. Of the three animals captured in arboreal trap sets, all were in Victor Traps. Placements included: at a 15° angle, about 25 cm off the ground and on a 4-cm-diameter vine; at a 30° angle, approximately 2 m above the ground and across two vines (6 and 13 cm diameter) growing around a tree; and at a 30° angle, 1.5 m off the ground and on a 1-cm-diameter vine. In the latter two cases, the animals were climbing up vines. Two males were found in pitfall buckets; one was found on the dawn trap check after a night of heavy rain. Three specimens were taken in Museum Specials placed on the ground, including a trap next to a tree with a 25 by 10-cm hole at the base (two separate individuals on consecutive nights) and one set in a 20-cm gap between two trees (1.5 and 1 m diameter). The only *Beamys* captured in the West Usambara was in the 5.5-ha fragment with the trap placed on the ground and in thick understory.

In the East Usambara, two males were collected in 1992 with abdominal testes measuring 4 by 2 mm and with non-

TABLE 2. External measurements (mm) and weight (g) of select rodent species collected during 1991–1993 surveys of the East and West Usambara Mountains, including total length (TL), head and body length (HB), length of tail vertebrae (TV), hind foot length (HF), ear length (EAR), and weight (WT). Given differences in measuring techniques between the two field collectors, measurements are presented separately. A one-way analysis of variance was used to test for sexual dimorphism, significant differences between the East and West Usambaras, or both. Only if significant differences were detected are samples presented separately, as well as associated statistical information.

Species	TL	HB	TV	HF	EAR	WT
Paraxerus vexillarius S.M.G., WU, ♀						
Mean ± SD	420.0 ± 25.46		196.0 ± 15.56	56.0 ± 1.0	20.3 ± 2.08	252.7 ± 64.94
Range	402–438		185–207	55–57	18–22	178–296
n	2		2	3	3	3
Dendromus mystacalis S.M.G., EU, ♀, ♂						
Mean ± SD	135.1 ± 12.00	60.0 ± 5.15	74.6 ± 7.33	15.2 ± 1.04	13.0 ± 1.07	5.7 ± 1.55
Range	114–149	51–68	64–86	14–17	11–14	3.5–8.5
n	8	8	8	8	8	8
Dendromus mystacalis W.T.S., EU, ♂						
Mean ± SD	129.7 ± 3.06	59.3 ± 3.06	69.7 ± 2.52	17.0 ± 1.00	10.7 ± 0.58	5.6 ± 0.47
Range	127–133	56–62	67–72	16–18	10–11	5.2–6.1
n	3	3	3	3	3	3
Beamys hindei S.M.G., EU, WU, ♀						
Mean ± SD	274.7 ± 6.90	140.7 ± 6.03	132.7 ± 8.54	22.7 ± 2.06	23.7 ± 2.06	59.5 ± 5.43
Range	269–284	135–147	122–141	20–25	21–26	53–65.5
n	4	4	4	4	4	4
Beamys hindei W.T.S., EU, ♀, ♂						
Mean ± SD	257.0 ± 36.33	135.0 ± 23.80	128.7 ± 11.41	24.7 ± 0.50	22.0 ± 0.82	58.7 ± 25.00
Range	219–291	110–160	114–140	24–25	21–23	38–93
n	4	4	4	4	4	4
Lophuromys aquilus S.M.G., EU, ♀						
Mean ± SD	199.2 ± 10.71	127.3 ± 8.16	68.9 ± 7.11	21.2 ± 1.26	18.8 ± 0.88	60.3 ± 11.07
Range	180–215	109–140	52–77	19–24	17–20	46–89
n	18	14	18	18	18	18
Lophuromys aquilus S.M.G., EU, ♂						
Mean ± SD	198.4 ± 12.16	124.0 ± 6.75	69.2 ± 8.40	21.7 ± 1.59	18.5 ± 1.17	58.0 ± 7.71
Range	172–216	110–137	45–84	18–24	16–20	41.5–73.5
n	28	21	28	28	28	28
Lophuromys aquilus W.T.S., EU, ♀						
Mean ± SD	193.3 ± 12.37	126.5 ± 7.29	69.6 ± 7.77	23.4 ± 1.03	17.5 ± 0.87	57.6 ± 10.99
Range	174–216	111–140	54–84	22–25	15–19	42–87
n	21	21	21	21	21	21
Lophuromys aquilus W.T.S., EU, ♂						
Mean ± SD	190.5 ± 10.84	124.6 ± 7.27	67.6 ± 4.40	23.5 ± 0.88	17.0 ± 0.84	57.6 ± 10.99
Range	172–214	110–137	59–77	22–25	14–18	42–87
n	28	28	28	28	28	21
Lophuromys aquilus S.M.G., WU, ♀						
Mean ± SD	198.0 ± 10.06	127.0 ± 7.07	66.9 ± 5.29	22.6 ± 1.40	18.6 ± 1.09	56.0 ± 8.20
Range	180–214	122–132	57–78	20–24	16–20	45.5–72
n	14	2	14	14	14	14
Lophuromys aquilus S.M.G., WU, ♂						
Mean ± SD	191.6 ± 12.98	123.0 ± 4.24	67.4 ± 7.63	22.3 ± 1.13	18.5 ± 1.51	52.8 ± 8.26
Range	169–210	120–126	47–78	20–24	17–23	40–69
n	16	2	16	16	14	16
Lophuromys aquilus W.T.S., WU, ♀						
Mean ± SD	191.5 ± 14.85	123.0 ± 9.90	68.0 ± 4.24	23.0 ± 0.00	17.0 ± 1.41	50.3 ± 10.96
Range	181–202	116–130	65–71	23–23	16–18	42.5–58
n	2	2	2	2	2	2
Lophuromys aquilus W.T.S., WU, ♂						
Mean ± SD	198.5 ± 12.02	127.0 ± 8.49	74.0 ± 5.66	22.0 ± 1.41	17.5 ± 0.71	56.0 ± 4.24
Range	190–207	121–133	70–78	21–23	17–18	53–59
n	2	2	2	2	2	2
Aethomys hindei S.M.G., WU, ♂	197		89	25	20	38.5
Grammomys ibeanus S.M.G., EU, WU, ♀, ♂						
Mean ± SD	296.0 ± 26.34	124	176.1 ± 17.17	24.2 ± 0.95	18.9 ± 1.37	44.4 ± 9.37
Range	240–361		140–220	22–26	17–21	27.5–60
n	19		20	20	19	19

TABLE 2. *Continued.*

Species	TL	HB	TV	HF	EAR	WT
Grammomys ibeanus W.T.S., EU, WU, ♀, ♂						
Mean ± SD	300.2 ± 14.13	121.4 ± 7.54	168.6 ± 24.11	24.6 ± 2.07	19.0 ± 1.22	46.3 ± 6.03
Range	279–315	112–130	129–194	21–26	17–20	39.5–51.5
n	5	5	5	5	5	5
Grammomys macmillani W.T.S., EU, ♀, ♂						
Mean ± SD	254.5 ± 24.46	107.8 ± 10.87	151.3 ± 14.89	23.3 ± 0.50	16.0 ± 1.63	38.9 ± 9.59
Range	230–288	97–119	136–171	23–24	14–18	30–51
n	4	4	4	4	4	4
Grammomys macmillani S.M.G., EU, WU, ♀, ♂						
Mean ± SD	265.1 ± 21.94	112.0 ± 9.38	155.4 ± 13.95	22.6 ± 1.34	17.8 ± 1.17	35.2 ± 9.98
Range	221–297	97–123	125–174	21–25	16–20	17.5–46.5
n	16	6	16	18	18	18
Hylomyscus arcimontensis S.M.G., EU, ♀						
Mean ± SD	221.4 ± 12.27	86.7 ± 7.17	132.7 ± 8.84	18.7 ± 0.78	18.2 ± 0.94	18.4 ± 3.63
Range	194–235	72–92	118–142	17–20	17–20	11–24.5
n	11	8	11	12	12	12
Hylomyscus arcimontensis S.M.G., EU, ♂						
Mean ± SD	225.0 ± 21.52	87.4 ± 10.91	136.0 ± 12.66	19.0 ± 1.00	18.1 ± 0.76	21.4 ± 5.39
Range	194–253	63–105	116–154	17–20	17–19	11–26.5
n	13	12	13	13	13	12
Hylomyscus arcimontensis W.T.S., EU, ♀						
Mean ± SD	231.7 ± 11.09	92.0 ± 5.10	141.6 ± 7.44	20.5 ± 0.71	17.7 ± 0.67	20.0 ± 3.65
Range	208–247	81–100	124–150	20–22	17–19	14–26
n	10	10	10	10	10	9
Hylomyscus arcimontensis W.T.S., EU, ♂						
Mean ± SD	222.9 ± 26.17	91.3 ± 12.22	137.4 ± 13.81	20.8 ± 1.09	17.0 ± 1.00	20.7 ± 5.93
Range	186–262	75–110	120–161	19–22	15–18	12–29
n	8	9	8	9	9	9
Hylomyscus arcimontensis S.M.G., WU, ♀						
Mean ± SD	222.5 ± 9.59	88.3 ± 5.06	134.1 ± 5.97	19.7 ± 0.98	17.8 ± 0.70	17.4 ± 2.72
Range	200–241	77–97	120–147	18–22	17–21	12.5–26.5
n	53	14	53	56	56	56
Hylomyscus arcimontensis S.M.G., WU, ♂						
Mean ± SD	226.5 ± 9.81	92.4 ± 3.97	135.1 ± 6.64	20.1 ± 0.92	17.8 ± 0.98	21.7 ± 4.07
Range	190–249	87–97	110–151	18–22	15–21	14–34
n	52	5	54	54	52	53
Hylomyscus arcimontensis W.T.S., WU, ♀						
Mean ± SD	214.7 ± 9.70	87.2 ± 4.69	130.8 ± 5.69	20.0 ± 0.53	16.5 ± 2.42	16.3 ± 2.35
Range	198–232	80–96	117–141	19–21	8–18	13.5–21
n	14	15	14	15	15	15
Hylomyscus arcimontensis W.T.S., WU, ♂						
Mean ± SD	228.1 ± 10.20	94.7 ± 4.29	138.5 ± 6.81	20.8 ± 0.70	17.0 ± 0.68	21.6 ± 2.50
Range	211–245	87–102	127–151	20–22	16-18	18–25
n	14	14	14	14	14	14
Mus musculoides S.M.G., WU, ♂	96		43	12	8	3
Mus musculoides W.T.S., EU, ♂	97	58	42	13	9	4.8
Rattus rattus S.M.G., EU, ♂	346	155	195	33	22	86
Rattus rattus W.T.S., EU, ♀, ♂						
Mean ± SD	344.0 ± 0.00	159.0 ± 1.41	194.0 ± 1.41	33.0 ± 1.41	21.0 ± 1.41	102.0 ± 1.41
Range	344–344	158–160	193–195	32–34	20–22	101–103
n	2	2	2	2	2	2
Graphiurus kelleni W.T.S., EU, ♂	134	79	55	18	13	14.5
Graphiurus murinus W.T.S., EU, WU, ♀, ♂						
Mean ± SD	167.1 ± 14.85	98.6 ± 2.62	71.1 ± 14.61	20.0 ± 1.41	15.0 ± 0.76	22.3 ± 2.67
Range	143–180	94–101	44–83	17–22	14–16	18.5–27
n	8	8	8	8	8	8
Graphiurus murinus S.M.G., WU, ♀, ♂						
Mean ± SD	168.8 ± 12.84	95.5 ± 3.54	79.2 ± 10.67	18.0 ± 1.27	15.1 ± 1.05	19.4 ± 2.56
Range	136–195	93–98	43–93	16–20	14–17	15–25.5
n	17	2	17	17	17	16

TABLE 3. External measurements (mm) and weight (g) of *Praomys delectorum* collected during 1991–1993 surveys of the East and West Usambara Mountains, including total length (TL), head and body length (HB), length of tail vertebrae (TV), hind foot length (HF), ear length (EAR), and weight (WT). Specimens were separated by field collector and sex. F values generated from a one-way analysis of variance are presented.

	TL	HB	TV	HF	EAR	WT
S.M.G.						
East Usambara						
Females						
Mean ± SD	223.7 ± 18.05	98.5 ± 6.67	123.2 ± 11.38	21.2 ± 1.31	20.0 ± 1.07	25.4 ± 5.81
Range	187–251	86–109	99–143	17–23	18–23	14.5–33.5
n	21	19	21	20	21	20
Males						
Mean ± SD	231.8 ± 17.61	103.0 ± 8.81	127.5 ± 10.75	22.5 ± 1.03	20.5 ± 1.17	29.0 ± 7.07
Range	190–262	85–116	104–145	21–24	18–22	15.0–42.5
n	21	20	21	21	21	20
F	2.2	3.2	1.5	13.1***	2.3	3.0
West Usambara						
Females						
Mean ± SD	216.0 ± 14.54		121.3 ± 7.80	21.5 ± 0.58	20.3 ± 0.96	20.5 ± 3.76
Range	196–229		110–128	21–22	19–21	17.5–26
n	4		4	4	4	4
Males						
Mean ± SD	234.1 ± 11.21		129.1 ± 6.23	22.5 ± 0.97	20.5 ± 1.17	24.6 ± 4.06
Range	213–249		118–138	21–25	18–22	15.5–30.5
n	9		10	13	12	12
F	6.1*		4.0	3.5	0.1	3.1
W.T.S.						
East Usambara						
Females						
Mean ± SD	209.7 ± 13.80	96.1 ± 6.63	116.1 ± 7.76	22.8 ± 0.70	18.7 ± 0.98	23.8 ± 6.23
Range	174–228	80–105	98–129	22–24	17–20	14.0–37.5
n	20	20	20	20	20	19
Males						
Mean ± SD	223.5 ± 20.77	101.4 ± 10.63	124.4 ± 11.62	23.7 ± 1.18	18.9 ± 1.05	28.1 ± 6.54
Range	162–258	75–115	90–148	21–26	16–20	14.5–39.5
n	30	33	30	33	33	33
F	6.9*	3.9	7.8**	10.2**	0.4	5.4*
West Usambara						
Females						
Mean ± SD	224.7 ± 7.51	97.8 ± 6.72	116.8 ± 14.38	22.8 ± 1.10	18.6 ± 1.14	22.8 ± 3.72
Range	216–229	90–108	96–135	21–24	17–20	19.5–29.0
n	3	5	5	5	5	5
Males						
Mean ± SD	231.0 ± 9.85	107.0 ± 2.65	127.0 ± 8.19	24.3 ± 1.15	20.3 ± 0.58	30.7 ± 2.25
Range	223–242	105–110	120–136	23–25	20–21	28.5–33.0
n	3	3	3	3	3	3
F	0.8	4.9	1.2	3.5	5.8	10.6*

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

convoluted epididymides. Six females were obtained: three with perforate vaginas and three imperforate. Only one out of five females dissected was pregnant (one embryo in the left uterine horn, three in the right, and the largest embryo with a crown–rump length of 6 mm), with five placental scars (two left, three right), and large teats. One of the other four females examined had placental scars (one left, three right) and was lactating. The West Usambara specimen was a nulliparous female.

Two lactating adult females were found on the same day in traps 5 m apart: one was on the ground at the base of a tree and the other on a vine 1.5 m off the ground. The following day, a subadult nulliparous female was captured in the trap set at the base of the tree. One of the *Beamys* captured in 1993 had seven fecal pellets in the large intestine that measured 8 by 5, 8 by 5, 8 by 4, 7 by 4.5, 6 by 4.5, 6 by 4, and 7 by 5 mm.

See Table 2 for external measurements. In the type description of *B. hindei*, Thomas (1909) stated that diagnostic characteristics of this species include six pads on all four feet and the fifth hind toe without a claw. The original description of *B. major* Dollman 1914, with the type series from Mt. Mulanje, Malawi, omits details on the foot pads or claws. However, Hanney and Morris (1962) described these characters from a series of *B. major* collected in Malawi. All 19 adult specimens they examined had six pads on the hind foot and five pads on the forefoot, and every digit had a claw, with the exception of the forefoot pollex with a nail. All of our specimens from the Usambara Mountains had the same claw condition as described for *B. major*. Some authorities consider *major* a subspecies of *B. hindei* (Hubbard, 1970; Ansell & Ansell, 1973; Corbet & Hill, 1991), whereas others suggest the

TABLE 4. Abundance of rodent species in forest fragments sampled in the East Usambara based on the proportional field effort in a given forest block. Results of X^2 tests compare expected to observed captures for each species in each fragment. Expected trap success is based on the null hypothesis of equal distribution across all fragments. Captures by techniques other than traps (i.e., pitfalls and animals brought to us by local people) are not included. Significantly higher abundance than expected in a given fragment is shown in bold.

	Site (trap-nights)											
Species	0.2A (150)	0.4 (75)	0.2B (150)	0.6 (370)	0.8 (300)	3.1 (200)	2.6 (150)	3.3 (460)	29.4 (450)	Control (2837)	Total (5142)	X^2
Beamys hindei			1							3	4	8.62
Grammomys macmillani	**4**			**5**		1					10	82.88***
Grammomys ibeanus					1					2	3	5.30
Hylomyscus arcimontensis									1	28	29	23.47**
Lophuromys aquilus	4	3	4	6	10	3	2	3	5	45	85	13.27
Mastomys natalensis										1	1	0.81
Praomys delectorum			3		10	4	1	15	13	**125**	178	24.54**
Rattus rattus									1	3	4	3.06
Graphiurus murinus	1				1					2	4	10.50
Total captures per site	9	3	8	18	22	8	3	18	20	**209**	318	20.31*
No. of species per site	3	1	3	3	4	3	2	2	4	8	9	

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

two forms may be distinct species (Ellerman, 1941; Hanney, 1965; Musser & Carleton, 2005). A critical study is needed to resolve this question.

SPECIMENS EXAMINED—**EAST USAMBARA**, 6 km NW Amani, Monga Tea Estate (TRL S—FMNH 150099); 4.5 km WNW Amani, Monga Tea Estate, control site (PF 33—FMNH 150100; TRL AN—FMNH 151223); 4.5 km ESE Amani, Monga Tea Estate, control site (PF 41—FMNH 150101; TRL AF—FMNH 150102, 150103, 150428; TRL AP—FMNH 151224); **WEST USAMBARA**, 11 km NW Korogwe, Ambangulu Tea Estate (TRL F—FMNH 147238).

Family Muridae: Subfamily Deomyinae
***Lophuromys aquilus* True, 1892**

DISTRIBUTION—*Lophuromys aquilus* was previously referred to in the literature as *L. flavopunctatus* Thomas, 1888 (Verheyen et al., 2002; Musser & Carleton, 2005). *Lophuromys aquilus* has a broad distribution in lowland and mesic montane habitats in eastern and some central African countries (including Democratic Republic of the Congo) and extends as far south as Angola. In Tanzania, it is found on most massifs with montane forests, except Mt. Meru, where the endemic *L. verhageni* W. Verheyen, Hulselmans, Dierckx and E. Verheyen, 2002, occurs; this latter species was also previously included within *L. flavopunctatus* (Musser & Carleton, 2005).

ECOLOGY AND REPRODUCTION—*Lophuromys aquilus* was among the most commonly trapped rodents in the East Usambara forests, second only to *Praomys delectorum*, and making up 26% of the total murids captured (Table 4). Capture rates of *L. aquilus* varied among sites; it was the most abundant rodent in fragments less than 5 ha, the second most abundant species in the 3.3- and 29.4-ha parcels, and ranked third in the control area.

Lophuromys aquilus was less abundant (based on trap success) in the West Usambara, compared with the East Usambara (Table 4), where it made up 12.4% of the total murids captured, exceeded by *P. delectorum* and *Hylomyscus arcimontensis*. The 1.9-ha fragment was the only forest site where *L. aquilus* was the most abundant trapped rodent; in the other parcels less than 5 ha, it was the second most abundant species. At the 37.8-ha and control sites, this species was distinctly less common.

Overall, 173 specimens were collected during this study, and with the exception of five individuals either captured by hand, tangled in a mist net, or found in a pitfall, all were in the trap lines. All trap sets that yielded this species were either on the ground or on slightly elevated surfaces with direct non-vertical access from the ground. There is no evidence of scansorial displacement in this species. *Lophuromys* was frequently captured in areas with moist soil and thick herbaceous vegetation. In 30 cases, two individuals were captured in the same trap set, and in five cases, three individuals were obtained in the same trap set.

Of the 173 animals captured, only four individuals were not sexed. The ratio of females to males was 78:91. Over the study, 26 females were examined for reproductive activity (four, 19, and three in 1991, 1992, and 1993, respectively); six (23.1%) were pregnant (1 [25%], 4 [21%], 1 [33%], respectively). The crown–rump length of the embryos ranged from 3 to 32 mm (mean = 20.8 mm). The testes of 32 males were examined, and the mean measurements were 9.4 by 6.0 mm, and 24 of 31 assessed (77%) had convoluted epididymides. In a sample from the West Usambara measured by S.M.G., the hind foot lengths of the males were significantly larger than those of females ($F = 8.1$, $P < 0.01$; Table 2). Based on this result, in Table 2, the external measurements are separated by sex and further subdivided by mountain and collector.

COMMENTS—Cunneyworth et al. (1996) reported captures of *Lophuromys sikapusi* (Temminck, 1853) at several sites in the Magoroto Forest Reserve, East Usambara, but listed no voucher specimens. The species name *L. sikapusi* was previously used for members of this genus occurring in the region (Swynnerton & Hayman, 1951), but after recent taxonomic changes, these records are almost certainly referable to *L. aquilus*.

SPECIMENS EXAMINED—**EAST USAMBARA**, 6 km NW Amani, Monga Tea Estate (TRL O—FMNH 150206, 150456, 150457, 150460; TRL P—FMNH 150459; TRL Q—FMNH 150207, 150458; TRL R—FMNH 150171, 150172, 150205, 150453, 150454, 150461; TRL S—FMNH 150173, 150179, 150208, 150464; TRL T—FMNH 150174–150178, 150455, 150462, 150465, 150466, 150471; TRL U—

FMNH 150463, 150467–150470; TRL W—FMNH 150180, 150181); 8 km NWN Amani, Bulwa Tea Estate (TRL AA—FMNH 150191, 150192, 150488; TRL AB—FMNH 150195, 150213, 150486; TRL AC—FMNH 150193, 150485; TRL AD—FMNH 150194, 150487, 150489, 150490); 4.5 km WNW Amani, Monga Tea Estate, control site (TRL M—FMNH 147303, 147509, 147512, 147513; TRL N—FMNH 147304, 147510, 147511, 147514; TRL X—FMNH 150479, 150482, 150483, 151483; TRL Y—FMNH 150182, 150183, 150185, 150186, 150209, 150210, 150472, 150473; TRL Z—FMNH 150184, 150187, 150189, 150190, 150211, 150474–150478, 150480, 150481; TRL AN—FMNH 151484, 151485; TRL AO—FMNH 151256, 151257, 151260, 151490, 151491; captured by hand—FMNH 150188, 150212); 4.5 km ESE Amani, Monga Tea Estate, control site (PF 64—FMNH 151494; TRL AF—FMNH 150196; TRL AG—FMNH 150197–150199, 150491; TRL AH—FMNH 150200–150202, 150492–150495; TRL AJ—FMNH 150496–150504; TRL AP—FMNH 151258, 151486, 151487, 151492, 151493; TRL AQ—FMNH 151255, 151262, 151488, 151489; captured by hand—FMNH 151261); **WEST USAMBARA**, 12.5 km NW Korogwe, Ambangulu Tea Estate (PF 4—FMNH 147491; TRL A—FMNH 147292, 147478; TRL G—FMNH 147293, 147479, 147481, 147483–147485; TRL H—FMNH 147295, 147480, 147482, 147486, 147489; TRL I—FMNH 147294, 147487, 147490; TRL K—FMNH 147297, 147298, 147494–147498, 147500, 147501, 147503; TRL L—FMNH 147301, 147504; TRL AK—FMNH 150214, 150215, 150506–150508; TRL AL—FMNH 150203, 150204; TRL AR— FMNH 151481, 151482); 14.5 km NW Korogwe, Ambangulu Tea Estate (TRL C—FMNH 147296, 147492, 147493, 147499, 147502); 11 km NW Korogwe, Ambangulu Tea Estate (TRL D—FMNH 147299, 147506, 147507; TRL E—FMNH 147300, 147505; TRL F— FMNH 147302, 147508).

Family Muridae: Subfamily Murinae

***Aethomys hindei* (Thomas, 1902)**

Distribution—*Aethomys hindei* has been reported from throughout eastern Africa, and as far west as Chad. It is not known south of Tanzania (Musser & Carleton, 2005). Kingdon (1974a) stated that this species is "certainly not a forest animal" but a grassland species. However, it has been captured in fallow areas at the edge of forests (Hubbard, 1972). Davis (1975) suggested that two morphological forms of *A. hindei* were found on either side of the Eastern Rift Valley. Swynnerton and Hayman (1951) considered *hindei* as a subspecies of *kaiseri* (Noack, 1887) and mentioned records from Amani and Magoroto (in the Tanga Region) and from Kibongoto (near Mt. Kilimanjaro). *Aethomys hindei* is also reported from Muheza village at the southeastern base of the East Usambara and in distinctly drier habitat (Hubbard, 1972).

Ecology and Reproduction—The single animal referable to this species we captured in the Usambara Mountains was a juvenile male taken in the West Usambara 1.9-ha fragment at 1171 m in disturbed montane forest. It was obtained in a Museum Special trap placed on the ground in leaf litter and slightly less than 100 m from the forest edge. The animal was found in the trap at 1500 h, suggesting diurnal activity. The testes were abdominal, measuring 4 by 2 mm, with non-convoluted epididymides.

In the Usambaras, *A. hindei* is unknown in undisturbed forest, and it is unclear to what extent it occurs at higher elevations in agricultural areas. Hubbard (1972) collected this species in July at 200 m in Muheza at the base of the East Usambara. Of the 16 females he obtained, 25% were pregnant. Table 2 reports external measurements of our trapped individual.

Comments—The single individual captured was a juvenile and based on cranio-dental measurements and characters it falls within the range of *A. hindei* (sensu Davis, 1975; see also Denys & Tranier, 1992). The incisors are opisthodont, the greatest length of the skull (30.5 mm) minus the condylobasal length (27.6 mm) is 2.9 mm, and the zygomatic width is 53% of the greatest length of the skull. We echo the call for a systematic review of the genus to define species limits of *A. kaiseri* and *A. hindei* (Musser & Carleton, 2005).

Specimens Examined—**WEST USAMBARA**, 11 km NW Korogwe, Ambangulu Tea Estate (TRL E—FMNH 147239).

***Grammomys ibeanus* (Osgood, 1910)**

Distribution—*Grammomys ibeanus* is known from northeastern Zambia to southern Sudan; it is found in different montane forests of eastern Tanzania, but the taxonomy of this presumed speeies group needs critical review (Stanley et al., 1998b; Musser & Carleton, 2005).

Ecology and Reproduction—A substantial proportion of the total 25 trapped individuals (13 females and 12 males) was obtained in the control sites of the East (66%) and West Usambaras (41%). In the East Usambara, three specimens were collected: two in the EU control site forest and the third in the 0.8-ha fragment. In thc West Usambara, six were collected in the 1.5-ha fragment, four in the 5.5-ha fragment, three in thc 37.8-ha fragment, and nine in the WU control site. Within the different habitats sampled in the WU control site, four *G. ibeanus* were collected in TRL H, placed in an area at the forest edge that had recently been cut and colonized by secondary vegetation; four in TRL B and TRL AR, characterized by relatively dry but pristine forest; and one in TRL AK with primary forest. We did not observe sympatric occurrence in the same forest fragment of *G. ibeanus* and *G. macmillani*.

In general, traps set on limbs associated with thick vegetation or trees were particularly successful in capturing *G. ibeanus*. Ground sets on moist soil in thick secondary and herbaceous vegetation were also productive. On more than one occasion, specimens were caught on consecutive nights in the same trap or neighboring traps. For example, in 1991, in the 37.8-ha West Usambara fragment, two females and one scrotal male were captured on two consecutive nights in Museum Specials set on 5–10-cm-diameter vines 1.5–2 m off the ground. All of these traps were within 30 m of the forest edge. In 1992, in the EU control site (TRL AH), two specimens of *G. ibeanus* were trapped on consecutive nights in the same Museum Special set on the ground—the first night (23 August 1992) a scrotal male and the following night a female without embryos or placental scars and with a perforated vagina. In the WU control site, in the TRL H line placed in secondary vegetation, four specimens were caught in the course of five consecutive nights in Museum Specials (two in the same trap) within 11 m from each other. In 1993, in the TRL AR line in the WU control site, two females (one nulliparous and one with eight placental scars) were taken on 20 August in two consecutive Museum Specials.

Of the two females collected in the East Usambara Mountains, one was nulliparous and the other, captured in the 0.8-ha fragment, had two embryos in the left and one in the right uterine horns, the largest of which was 10 mm in crown–rump length. The one male had scrotal testes that measured 15 by 10 mm and convoluted epididymides. In the

West Usambara, none of five females checked was pregnant, and of the four examined for previous reproductive activity, three had two and two, two and three, and two and six placental scars in the left and right uterine horns, respectively. The fifth individual was nulliparous.

Specimens Examined—**EAST USAMBARA**, 6 km NW Amani, Monga Tea Estate (TRL T—FMNH 150105); 4.5 km ESE Amani, Monga Tea Estate, control site (TRL AH—FMNH 150106, 150107); **WEST USAMBARA**, 11 km NW Korogwe, Ambangulu Tea Estate (TRL D—FMNH 147246, 147248, 147415, 147418, 147420, 147422; TRL F—FMNH 147247, 147416, 147417, 147419); 12.5 km NW Korogwe, Ambangulu Tea Estate (TRL H—FMNH 147240–147242, 147405; TRL B—FMNH 147244, 147410; TRL AK—FMNH 150108; TRL AR—151235, 151236); 14.5 km NW Korogwe, Ambangulu Tea Estate (TRL C—FMNH 147245, 147412, 147413).

Grammomys macmillani (Wroughton, 1907)

Distribution—*Grammomys macmillani* is reported from Sierra Leone to Tanzania and south to Zimbabwe, but the precise geographical limits of its distribution are unresolved (Musser & Carleton, 2005). Within Tanzania, the species has been found in both lowland (e.g., Minziro Forest) and montane forest localities (South Pare) (Stanley et al., 1998a; Stanley & Foley, 2008). Matschie (1915) described *G. m. usambarae* based on a specimen collected in Amani in 1911.

Ecology and Reproduction—In total, 22 specimens were obtained in the East and West Usambaras during this study. Seven females and four males were captured in the East Usambara, and five females and four males (for two specimens, the sex was not determined) in the West Usambara. In contrast to *G. ibeanus* (see above), which was often found in large, relatively non-degraded forest fragments, all specimens of *G. macmillani*, with one exception, were captured in forest fragments under 2 ha or in disturbed habitat. The exception was an individual trapped in PF 3 in the WU control site forest. In the East Usambara, five of the 11 (45%) were captured in the 0.6-ha fragment, four (36%) in the 0.2A-ha fragment, one in the 3.1-ha fragment, and one in PF 57 placed in tea habitat. In the West Usambara, six of the 11 collected (55%) were in TRL I, and single individuals were captured in TRL J and PR 10 (both in the 1.8-ha fragment), and TRL H and PF 3 (both in the WU control site).

Whereas *G. ibeanus* was obtained almost exclusively in arboreal sets, *G. macmillani* seems to be more terrestrial in its substrate use. However, four of the 11 (36%) individuals of *G. macmillani* caught in the East Usambara were in traps set 1–2.5 m above the ground, whereas in the West Usambara, two of the 11 (18%) specimens captured were taken in arboreal sets. In the 0.2A - and 0.6-ha fragments of the East Usambara, traps on the ground that yielded *G. macmillani* include Museum Specials set next to logs, tree buttresses, or vine tangles and placed either on the forest edge or toward the interior of the fragment. Traps set in thick vegetation, consisting of both woody and herbaceous vines, were particularly productive for this species. Ecotonal areas between forest and agricultural land, such as TRL I produced numerous individuals of *G. macmillani*.

All but one of the seven females of *G. macmillani* captured in the East Usambara sites were pregnant or had evidence of past pregnancies. Four had four and zero, one and two, zero and five, and three and one embryos in the left and right uterine horns, the largest having crown–rump lengths of 17, 24, 10, and 5 mm, respectively. Two non-pregnant females had two and zero and three and two placental scars in the left and right uterine horns, respectively. The remaining individual was nulliparous. Only one of five females captured in the West Usambara sites was examined, and it was nulliparous. The reproductive status of three of four males captured in the East Usambara was assessed: one had abdominal testes (8 by 4 mm), and two had scrotal testes (9 by 6 and 8 by 4 mm). All had non-convoluted epididymides. Four males collected in the West Usambara were examined for reproductive condition: one had scrotal testes (9 by 3 mm), and three had abdominal testes, one of which measured 6 by 4 mm. See Table 2 for external measurements.

Specimens Examined—**EAST USAMBARA**, 6 km NW Amani, Monga Tea Estate (TRL O—FMNH 150111–150114; TRL R—FMNH 150109, 150110, 150115, 150116, 150372; TRL AA—FMNH 150117); 4.5 km WNW Amani, Monga Tea Estate, control site (PF 57—FMNH 151476); **WEST USAMBARA**, 11 km NW Korogwe, Ambangulu Tea Estate (PF 10—FMNH 147414; TRL E—FMNH 147421); 12.5 km NW Korogwe, Ambangulu Tea Estate (PF 3—FMNH 147404; TRL G—FMNH 147249, 147406; TRL I—FMNH 147250, 147408, 147409, 147411; TRL J—FMNH 147243; TRL H—FMNH 147407).

Hylomyscus arcimontensis Carleton & Stanley, 2005

Distribution—This species is distributed across montane islands throughout eastern and southern Tanzania and may extend into northern Malawi (Carleton & Stanley, 2005). Within Tanzania, *H. arcimontensis* occurs on all Eastern Arc Mountains (and Mt. Rungwe) but is not known from the Taita Hills of Kenya or from geologically recent northern volcanoes such as Mt. Kilimanjaro and Mt. Meru.

Ecology and Reproduction—Over the three-year study in the Usambaras, 187 specimens of *H. arcimontensis* were captured, including 45 in the East and 141 in the West, which composed 9.9% and 21.3% of the total rodents captured on each massif, respectively. This species was the third and second most common rodent in the East and West Usambara Mountains, respectively.

The large samples of this taxon collected on each massif allow for the examination of patterns of sexual and geographic variation. A one-way analysis of variance was computed to determine whether this species shows sexual dimorphism in external measurements. More than 50 specimens of each sex were measured by S.M.G. in the West Usambara in 1991 and 1992. Males were larger than females in total length ($F = 4.4$, $P = 0.04$) and weight ($F = 41.7$, $P < 0.0001$). Tail, hind foot, and ear length measurements did not differ significantly between the sexes. Measurements recorded by S.M.G. from both the East and West Usambaras were compared for differences between the massifs. Total length and hind foot length were larger in females from the West than females from the East ($F = 12.6$, $P < 0.001$), and a similar pattern for the same variables was found in males ($F = 19.3$, $P < 0.0001$). Descriptive statistics for measurements divided by sex, collector, and massif are presented in Table 2.

Comments—Almost all of the specimens from the East Usambara were collected in the EU control site, suggesting microhabitat preferences, related presumably to forest size and vegetation composition. The single exception was an animal (FMNH 150139) captured in a tea plantation approximately 30 m from the 0.6-ha fragment that may have been dispersing between forest blocks. Abundance of this species, as measured by trap success, was notably lower on other Eastern Arc

Mountains (compared with the Usambaras) which possess relatively smaller amounts of remaining natural forest, such as the North Pare and Nguu Mountains (Stanley et al., 2007a; W. T. Stanley, unpubl. data).

Specimens Examined—**EAST USAMBARA**, 6 km NW Amani, Monga Tea Estate (TRL U—FMNH 150118; TRL V—FMNH 150139); 4.5 km WNW Amani, Monga Tea Estate, control site (TRL M—FMNH 147290, 147291, 147475, 147477; TRL N—FMNH 147476; TRL X—FMNH 150119; TRL AO—FMNH 151240, 151251); 4.5 km ESE Amani, Monga Tea Estate, control site (PF 41—FMNH 150141; TRL AF—FMNH 150140, 150142; TRL AG—FMNH 150143, 150429–150431, 150435; TRL AH—FMNH 150120–150125, 150147, 150148, 150432–150434; TRL AI—FMNH 150144–150146, 150149–150153, 150436; TRL AP—FMNH 151250, 151252, 151480; TRL AQ—FMNH 151246–151248, 151479); **WEST USAMBARA**, 12.5 km NW Korogwe, Ambangulu Tea Estate (TRL A—FMNH 147251, 147425–147427, 147431, 147432; TRL B—FMNH 147253–147258, 147262–147264, 147274–147277, 147333, 147435–147439, 147443, 147444, 147447–147453; TRL G—FMNH 147442, 147445; TRL H—FMNH 147252, 147259–147261, 147265–147270, 147423, 147424, 147428–147430, 147433, 147434, 147440, 147441, 147454–147456, 147459–147466, 147468; TRL I—FMNH 147271–147273, 147446; TRL J—FMNH 147457, 147458; TRL AK—FMNH 150154, 150156, 150159–150164, 150166, 150169, 150170, 150448–150452; TRL AL—150126–150138, 150155, 150167, 150168, 150437–150447; TRL AR—151243–151245, 151478); 14.5 km NW Korogwe, Ambangulu Tea Estate (TRL C—FMNH 147278–147289, 147469–147473, 147642); 11 km NW Korogwe, Ambangulu Tea Estate (TRL F—147474).

Mastomys natalensis (Smith, 1834)

Distribution—*Mastomys natalensis* is distributed across much of sub-Saharan Africa. This species is ubiquitous in lowland agricultural areas across Tanzania and is a crop pest.

Ecology and Reproduction—All 13 specimens collected during this study were captured on the ground, and 12 specimens were caught in 1991 in the West Usambara. Ten animals were collected in TRL G, placed in a fallow agricultural area. A female and a scrotal male were taken on two consecutive days in adjacent Victor Traps in TRL I (the Grid site line) in an area with thick vegetation next to a small rock outcrop. No other habitat sampled in the WU resulted in the capture of *Mastomys*. One specimen was collected in 1992 in the EU control site in TRL AF within closed canopy forest and with an open understory. This reproductively active male was taken 43 m from the forest edge in a Museum Special set in a subterranean root tangle, 50 cm below the level of the ground. This record is atypical, particularly given that we caught no other individual of this rodent in the East Usambara, and those obtained in the West Usambara were all captured in disturbed habitats.

Two of the 13 specimens were not sexed, and the one female examined had a perforate vagina and large mammae. Seven of the nine males captured had scrotal testes measuring 7–15 by 4–8 mm, and four individuals had convoluted epididymides.

Specimens Examined—**EAST USAMBARA**, 4.5 km ESE Amani, Monga Tea Estate, control site (TRL AF—FMNH 150104); **WEST USAMBARA**, 12.5 km NW Korogwe, Ambangulu Tea Estate (TRL G—FMNH 147305–147308, 147515–147517, 147538, 147589, 147590; TRL I—FMNH 147329, 147518).

Mus musculoides Temminck, 1853

Distribution—*Mus musculoides* occurs across much of sub-Saharan Africa but is unknown in the southern African subregion, where it is replaced by *M. minutoides* Smith, 1834 (Musser & Carleton, 2005; but see Veyrunes et al., 2005).

Ecology and Reproduction—Two males were captured during this study in 1991 and 1992: one in the West Usambara in a *Eucalyptus* plantation and one in the East Usambara in a tea plantation. External measurements are given in Table 2.

Specimens Examined—**EAST USAMBARA**, 6 km NW Amani, Monga Tea Estate (PF 16—FMNH 150216); **WEST USAMBARA**, 11 km NW Korogwe, Ambangulu Tea Estate (PF 10—FMNH 147519).

Praomys delectorum (Thomas, 1910)

Distribution—*Praomys delectorum* is distributed within the Tanganyika–Nyasa Montane Forest formation (Moreau, 1966), including montane ranges in Zambia, Malawi, Tanzania, and southeastern Kenya (Musser & Carleton, 2005). Within Tanzania, it is known from all Eastern Arc Mountains, as well as northern volcanoes (Kilimanjaro, Meru, Ngorongoro) and within the Southern Highlands, but does not occur in mountains associated with the Albertine Rift, such as Mahale or Mbizi, where *P. jacksoni* de Winton, 1897, is found (Stanley et al., 1998b; Musser & Carleton, 2005). *Praomys delectorum* has been recorded as low as 300 m in forests at the foot of the East Usambara (Stanley et al., 2005).

Ecology and Reproduction—To assess whether sexual dimorphism exists in external measurements of *Praomys delectorum*, samples collected from the East and West Usambaras, segregated by collector, were tested for significant differences (Table 3). Males were larger than females in all compared variables. These differences were significant in measurements recorded by both S.M.G. and W.T.S. for the hind foot length in the East Usambara sample; by W.T.S. for total length, tail length, and weight for the East Usambara sample; by S.M.G. for total length for the WU sample; and by W.T.S. for weight for the WU sample. Based on these results, the sexes are separated in statistical comparisons between mountains.

Only one of 17 females (5.9%) examined over the three-year survey was pregnant; this animal was one of 10 dissected in 1991 and had a single embryo in the left and three embryos in the right uterine horn, with the largest crown–rump length at 5 mm. In 1992, seven females were examined for reproductive condition and not a single individual in 1993. No lactating females were recorded.

The testes of 15 males were measured in 1991; the average measurements were 12.0 mm ± 2.9 (range = 5–17) by 6.1 mm ± 1.6 (range = 2–8). Thirteen of the 17 individuals had convoluted epididymides. In 1992, 16 males were examined, and the average measurements were 13.7 mm ± 1.8 (range = 11–17) by 7.1 mm ± 1.0 (range = 6–9). All had convoluted epididymides. In 1993, the average testes measurements of five males examined were 11.0 mm ± 3.3 (range = 6–14) by 6.6 mm ± 2.1 (range = 3–8), and four of five had convoluted epididymides.

In a study conducted between 2004 and 2006, Makundi et al. (2006) found a significant density increase in *Praomys delectorum* sampled in the Magamba Forest, West Usambara, between March and June compared with between September and December. The greatest number of males with scrotal testes and females with perforate vaginas were found from April to June. Based on these observations, as well as our data, little reproductive activity occurs during the dry period (July–

August), this species apparently has a relatively narrow period of annual breeding.

Specimens Examined—**EAST USAMBARA**, 6 km NW Amani, Monga Tea Estate (TRL P—FMNH 150217–150219, 150221, 150224, 150514, 150515; TRL Q—FMNH 150295, 150297, 150299–150301, 150511–150513; TRL R—FMNH 150220, 150292–150294, 150296, 150298; TRL S—FMNH 150225, 150226, 150509; TRL T—FMNH 150222, 150223, 150303–150307, 150516, 150517, 150519; TRL U—FMNH 150308–150315, 150520–150524); 8 km NWN Amani, Bulwa Tea Estate (TRL AA—FMNH 150332, 150333, 150540, 150541; TRL AC– FMNH 150257); 4.5 km WNW Amani, Monga Tea Estate, control site (TRL M—FMNH 147337, 147576–147578; TRL N—FMNH 147336, 147338; TRL X—FMNH 150231, 150316, 150318–150330, 150536–150539, 151278, 151282; TRL Y—FMNH 150228, 150229, 150232, 150245, 150246, 150249–150252, 150529, 150530; TRL Z—FMNH 150227, 150230, 150233–150236, 150238–150244, 150247, 150248, 150253–150256, 150525–150528, 150531, 150532, 150534, 150535; TRL AM—FMNH 151284, 151309; TRL AN—FMNH 151276, 151277, 151280, 151281, 151283, 151515, 151516, 151518–151527; TRL AO—FMNH 151297–151301, 151308, 151517, 151529); 4.5 km ESE Amani, Monga Tea Estate, control site (TRL AF—FMNH 150265, 150336–150340, 150552, 150559–150561, 150563, 150564, 150570; TRL AG—FMNH 150258–150264, 150334, 150542–150551, 150562, 150565–150569, 150573; TRL AH—FMNH 150266–150279, 150553–150558; TRL AI—FMNH 150341, 150342, 150344–150349; TRL AJ—FMNH 150343, 150571, 150572; TRL AP—FMNH 151285, 151302–151307, 151530–151533; TRL AQ—FMNH 151279, 151286–151296, 151310); **WEST USAMBARA**, 12.5 km NW Korogwe, Ambangulu Tea Estate (TRL A—FMNH 147309–147312, 147314, 147315, 147521–147523, 147527–147529, 147531, 147543; TRL B—FMNH 147317–147319, 147321–147323, 147325, 147330–147332, 147533–147537, 147541, 147542, 147545–147556, 147559, 147560; TRL G—FMNH 147313, 147539, 147540, 147557; TRL H—FMNH 147316, 147320, 147326, 147524–147526, 147530, 147532, 147544; TRL I—FMNH 147558, 147563, 147564; TRL J—FMNH 147324, 147327, 147328, 147561, 147562; TRL K—FMNH 147569–147571; TRL AK—FMNH 150157, 150158, 150165, 150350–150355, 150357–150362, 150583–150601; TRL AL—FMNH 150280–150291, 150356, 150574–150582; TRL AR—FMNH 151271, 151272, 151274, 151275, 151502–151512); 14.5 km NW Korogwe, Ambangulu Tea Estate (TRL C—FMNH 147334, 147565–147568, 147572, 147573); 11 km NW Korogwe, Ambangulu Tea Estate (TRL D—FMNH 147335, 147575; TRL F—FMNH 147574).

Rattus rattus (Linnaeus, 1758)

Distribution—As in other areas of east Africa, Tanzanian populations of this introduced species are found in areas associated with human habitation and only occasionally in natural forest.

Ecology and Reproduction—*Rattus* was rarely captured during our surveys in the Usambaras; only four specimens were taken during the three years. These four were obtained in the East Usambara between 25 July and 3 August 1992, along creeks with running water, in settings similar to where the species was trapped at 300 m in Kwamgumi Forest Reserve at the base of the East Usambara (Stanley et al., 2005). In the 29.4-ha parcel, one specimen was taken in a Victor Trap placed on a flat rock in a streambed within 130 m of the forest edge. Three others were collected in two Victor Traps and one Museum Special in a forested area dominated by the invasive tree *Maesopsis* and within a 32-m stretch of a 358-m-long trap line. All traps successful for this genus were on the ground, in the understory, and in areas with moist soil and thick herbaceous vegetation. Three males and one female were collected, and two of the males were examined for reproductive activity: one was scrotal and the other, a juvenile, had abdominal testes. External measurements of these animals are presented in Table 2.

Comments—*Rattus* was notably uncommon in natural forests of the Usambaras, as is the case in other montane forests of Tanzania (Stanley et al., 2005; Stanley & Hutterer, 2007; Mulungu et al., 2008; W. T. Stanley, unpubl. data). Matschie (1915) described *R. r. rattiformis* from Amani.

Specimens Examined—**EAST USAMBARA**, 4.5 km WNW Amani, Monga Tea Estate, control site (TRL Z—FMNH 150602, 150603, 150605); 6 km NW Amani, Monga Tea Estate (TRL U—FMNH 150604).

Family Gliridae: Subfamily Graphiurinae

Graphiurus kelleni (Reuvens, 1890)

Distribution—*Graphiurus kelleni* is known from savannah habitats across much of sub-Saharan Africa, from Senegal to Somalia and south to Mozambique (Holden, 2005). Within Tanzania, it has been previously reported in the Kwamgumi Forest Reserve at 230 m at the foot of the East Usambara (Stanley et al., 2005) and at Kibongoto at 1290 m on the slopes of Mt. Kilimanjaro (Swynnerton & Hayman, 1951).

Ecology and Reproduction—One male was collected in the control area of the East Usambara in 1993. The animal was obtained in a Museum Special set in an area of open understory, approximately 25 cm off the ground, and on a large tree buttress that extended into the upper canopy. The trap was about 170 m from the forest edge. The animal's testes were abdominal and measured 4 by 2 mm, and the epididymides were non-convoluted.

Comments—The single specimen, an adult, was identified to species based on its small size and blond fur coloration and was confirmed by comparison with other FMNH specimens of *G. kelleni* from the Arusha area identified by M. E. Holden. The only example of this species was taken in the EU control site, where it occurs in sympatry with *G. murinus*.

Specimens Examined—**EAST USAMBARA**, 4.5 km ESE Amani, Monga Tea Estate, control site (TRL AQ—FMNH 151364).

Graphiurus murinus (Desmarest, 1822)

Distribution—*Graphiurus murinus* is found in eastern, central, and southern Africa, from Ethiopia south to South Africa, and as far west as Democratic Republic of Congo (Holden, 2005).

Ecology and Reproduction—*Graphiurus murinus* was trapped in nearly equal proportions with arboreal (often in the same traps that yielded *Grammomys ibeanus*, *G. macmillani*, and *Hylomyscus arcimontensis*) and ground sets. In the East Usambara, three specimens of *Graphiurus murinus* were collected in three different arboreal sets and two ground sets. Terrestrially placed traps that yielded this species included a Victor Trap at the base of a tree with a hole in the 0.2A-ha fragment, and a Victor Trap next to a buttress of a large tree in the EU control site. The arboreal sets included a Museum Special wedged between a 1-m-diameter tree and a 7-cm-diameter stump about 35 cm off the ground in the 0.8-ha fragment. Two arboreal sets in the EU control area included a Museum Special oriented at 60° on a 4-cm-diameter vine circling a 50-cm-diameter tree, 1.5 m above the ground, and a Museum Special placed 1.3 m off the ground in an 80 by 10-cm hole in the side of a 30-cm-diameter tree.

In the West Usambara, *G. murinus* was captured in the 37.8-ha fragment and the WU control area (both in forest and on the edge of disturbed habitat), but not in the smaller forest fragments. Successful ground sets were in dense growth of bracken fern at the ecotone between forest and fallow agricultural land, inside hollows at the base of trees, and next to or under large rocks. Two males were captured at Ambangulu in 1992 over three consecutive nights in traps set 1 m apart and in close vicinity to exposed rocks. Successful arboreal trap sets in the West Usambara include those in large shrubs and on horizontal limbs ranging from 5 to 30 cm diameter, some surrounded by thick vegetation and others spanning open understory.

Three specimens of each sex were captured in the East Usambara between 1992 and 1993, and all were dissected to ascertain reproductive condition. No female was pregnant; one showed evidence of previous reproduction (one placental scar in the right uterine horn). The three males had abdominal testes measuring 4–6 by 2–3 mm with non-convoluted epididymides.

Fifteen specimens were collected in the West Usambara in 1991 (six males, nine females). Three females showed no signs of active reproduction; one had placental scars (three in the left uterine horn, one in the right). The testes of the four males examined were abdominal and measured 3–5 mm by 2–3 mm, and the epididymides were non-convoluted. Three males collected in 1992 were not scrotal, testes measured 4–10 by 2–4 mm, and the epididymides were non-convoluted. The two specimens captured in 1993 were female, and the single individual dissected was nulliparous.

Comments—One-way analyses of variance found no significant differences between the sexes in external measurements taken by a single collector (Table 2). The only significant difference between populations in the East and West Usambaras was the hind foot length (EU mean = 20.6 mm, n = 5; WU mean = 18.1, n = 20; $F = 14.6$, $P < 0.001$) and weight (EU mean = 23 g, n = 5; WU mean = 19.7, n = 19; $F = 6.3$, $P < 0.05$). We attribute these differences to the small sample size from the EU, and, in the case of the hind foot length, difference in measurement techniques between field collectors (see Stanley et al., this volume b). The descriptive statistics for these comparisons are presented in Table 2.

Specimens Examined—**EAST USAMBARA**, 6 km NW Amani, Monga Tea Estate (TRL O—FMNH 150363; TRL T—FMNH 150364); 4.5 km ESE Amani, Monga Tea Estate, control site (TRL AF—FMNH 150365; TRL AG—FMNH 150366; TRL AP—FMNH 151363); **WEST USAMBARA**, 14.5 km NW Korogwe, Ambangulu Tea Estate (TRL C—FMNH 147345, 147346); 12.5 km NW Korogwe, Ambangulu Tea Estate (TRL A—FMNH 147339, 147579, 147581; TRL B—FMNH 147583; TRL H—FMNH 147340–147343; TRL I—FMNH 147344, 147584; TRL AK—FMNH 150367–150369; TRL AR—FMNH 151362, 151542).

Family Bathyergidae: Subfamily Bathyerginae
Heliophobius argenteocinereus Peters, 1846

Distribution—*Heliophobius argenteocinereus* is only known from eastern and central Africa, from Zimbabwe to Tanzania and as far west as the Democratic Republic of the Congo, but it appears absent from Uganda (Kingdon, 1974a).

Ecology and Reproduction—Seven specimens (three females, four males) were collected in the West Usambara between 19 and 22 July 1991, and two females were collected in the East Usambara on 21 July and 12 August 1992. All animals were taken in agricultural fields, where the species is considered a pest. Table 2 reports external measurements.

From the 1991 collections, the testes of two males were 10 by 6 mm and 10 by 7 mm, and the epididymides of both animals were convoluted; the single female dissected had no embryos, but two placental scars in each uterine horn. The female collected 21 July 1992 was not pregnant, but the individual from 12 August of the same year had three embryos in each uterine horn, the largest of which had a crown–rump length of 6 mm.

Specimens Examined—**EAST USAMBARA**, 6 km NW Amani, Monga Tea Estate (captured by hand—FMNH 150370); 8 km NWN Amani, Bulwa Tea Estate (captured by hand—FMNH 150371); **WEST USAMBARA**, 14.5 km NW Korogwe, Ambangulu Tea Estate (captured by hand—FMNH 147347–147349, 147586); approximately 14 km NW Korogwe, Ambangulu Tea Estate, near Kunga village (captured by hand—FMNH 147350); 15 km NW Korogwe, near Bungo village (captured by hand—FMNH 147587, 147588).

Discussion

The Rodent Fauna of the East and West Usambara Mountains

Three years of fieldwork (1991–1993) documented 15 rodent species during relatively intensive small mammal surveys in montane portions of the East (13 species) and West Usambara Mountains (12 species). Of these 15 taxa, two (*Paraxerus vexillarius* and *Heliophobius argenteocinereus*) were only taken by hand, and the 1132 specimens collected with our standard trap and pitfall regimes represent 13 rodent species (12 in the East and 10 in the West Usambaras). All *Dendromus* specimens (n = 11) were obtained in pitfall devices. Most rodents collected (96.6%) during the Usambara work were taken in traps and relatively few in pitfall buckets, and as demonstrated previously at other sites in Tanzania (Stanley et al., 1996, 1998a,b), the combination of trap and bucket lines is an effective way to sample most small- to medium-sized rodents. However, larger scansorial and canopy-restricted (squirrels), and fossorial (mole rats) species were not captured with our trapping methodology.

Five species were observed on only one of the two Usambara massifs, with the genera *Aethomys* and *Paraxerus* only being collected in the West Usambara; *Dendromus*, *Rattus*, and *Graphiurus kelleni* were restricted to the East Usambara. Kingdon (1974a) stated that *P. vexillarius* is only known from the West Usambara, but recently, animals have been collected in the Nguru and Rubeho Mountains closely resembling this taxon (W. T. Stanley, unpubl. data; specimens in FMNH). Although *P. vexillarius* has not been recorded in the East Usambara Mountains, *P. palliatus* (Peters, 1852) has been observed at Amani (Swynnerton & Hayman, 1951) and Bombo Valley near the Bombo Forest Reserves (Cordeiro & Githiru, 2000). Kingdon (1974a) suggested that *P. vexillarius* might be a hybrid between *P. lucifer byatti* (Kershaw, 1923) (referred to as *P. vexillarius byatti* by Thorington & Hoffman [2005]), which is distributed on the Kilimanjaro, Usambaras, Uluguru, and Udzungwa massifs, and *P. palliatus*. Additional specimens from different localities and detailed morphological and molecular work are needed to adequately test this hypothesis. However, given phenotypically similar specimens referable to *P. vexillarius* from the West Usambara, Nguru, and Rubeho massifs, covering an expanse of approximately

TABLE 5. Abundance of rodent species in forest fragments sampled in the West Usambara based on the proportional field effort in a given forest block. Expected observations based on total number of trap-nights. Results of X^2 tests compare expected to observed captures for each species in each fragment, and expected trap success is based on the null hypothesis of equal distribution across all fragments. Captures by techniques other than traps (i.e., pitfalls and animals brought to us by local people) are not included. Success that was greater than expected in a given fragment is shown in bold.

Species	Site (trap-nights)					Total (2810)	X^2
	1.5 (186)	1.9 (174)	5.5 (350)	37.5 (650)	Control (1450)		
Beamys hindei			1			1	6.69
Aethomys kaiseri		**1**				1**	15.67**
Grammomys macmillani		1				1**	13.28**
Grammomys ibeanus	**6**		**4**	3	2	15***	32.12***
Hylomyscus arcimontensis			1	**18**	**34**	53**	15.96**
Lophuromys aquilus	**3**	**2**	**2**	**5**	2	14*	10.81*
Praomys delectorum	2		1	7	**46**	56***	24.18***
Graphiurus murinus				2	4	6	2.13
Total captures per site	11	4	9	35	88	147	
No. of species per site	3	2	5	5	5	9	

** $P < 0.01$.

*** $P < 0.001$.

250 km, such a large zone of introgression between these two forms seems unlikely.

Aethomys has been previously collected at 190 m near Muheza at the foot of the East Usambara (Hubbard, 1972), and excluding our exceptional West Usambara record from 1171 m and those of Makundi et al. (2006) at Magamba above 1500 m, there appear to be no records from across a broad elevational zone on these massifs. Given that dry habitat species such as *Mastomys natalensis* were found in the forests near Amani during our survey, *Aethomys* may also occur in the Amani area and was simply missed. *Rattus rattus* is a common commensal in portions of Tanzania, as previously reported from Korogwe (Swynnerton & Hayman, 1951). Hence, its occurrence in the Ambangulu area in areas of human habitation is expected. In Madagascar, *R. rattus* has colonized areas of undisturbed montane forests considerable distances from human settlements (e.g., Goodman et al., 1997; Goodman & Carleton, 1998), but after extensive rodent surveys of montane forests of Tanzania (Stanley et al., 1998b, 2000; Stanley & Hutterer, 2007; W. T. Stanley, unpubl. data), no parallel pattern was found.

Even though *Graphiurus kelleni* is considered a savannah species (Holden, 2005), this habitat characterization is too generalized based on a specimen captured within pristine forest of the EU control site, and one from the intact Kwamgumi Forest Reserve, composed of lowland forest, at 230 m at the foot of the East Usambara (Stanley et al., 2005). *Dendromus mystacalis* is adapted to areas of cultivation (Kingdon, 1974a), and probably has a broader distribution in agricultural areas of the West Usambara than our data indicated.

Rodents in Fragments versus Control Areas

Based strictly on our trapping results (excluding *Heliophobius* and *Paraxerus*), some rodent species favored specific habitats. Examples of such preferences include *Dendromus mystacalis* in tea plantations and, with one exception, *Mastomys natalensis* and *Mus musculoides* in fallow agricultural areas. All remaining rodent species were captured in forests of different sizes (Tables 4 and 5).

Overall, the most common rodent species in the East Usambara fragments, ranked by total number of captures, are *Praomys delectorum* (56.0%); *Lophuromys aquilus* (26.7%); *Hylomyscus arcimontensis* (9.1%); and *Grammomys macmillani* (3.1%); *Beamys hindei*, *Rattus rattus*, and *Graphiurus murinus* (1.2% each); *Grammomys ibeanus* (0.9%); and *Mastomys natalensis* (0.3%). Different fragments, however, have different relative abundance rankings (Table 6). In the West Usambara, the overall ranking, based on total trap captures, was *P.*

TABLE 6. Ranking (1 = most abundant) of most common rodent species in each of the fragments surveyed in the East Usambara.

Species	Site (trap-nights)									
	0.2A (150)	0.4 (75)	0.2B (180)	0.6 (370)	0.8 (360)	3.1 (200)	2.6 (180)	3.3 (460)	29.4 (450)	Control (972)
Beamys hindei			3							4
Grammomys macmillani	1[1]			3		3				
Grammomys ibeanus					2[1]					
Hylomyscus arcimontensis									3[1]	2
Lophuromys aquilus	1[1]	1	1	2	1[1]	2	1	2	2	3
Mastomys natalensis										6
Praomys delectorum			2	1	1[1]	1	2	1	1	1
Rattus rattus									3[1]	
Graphiurus murinus	2				2[1]					5
No. of species	3	1	3	3	4	3	2	2	4	6

[1] Rank shared by more than one species.

TABLE 7. Ranking (1= most abundant) of most common rodent species in each of the fragments surveyed in the West Usambara.

Species	Site (trap-nights)				
	1.5 (186)	1.9 (174)	5.5 (350)	37.5 (650)	Control (1400)
Beamys hindei			3[1]		
Aethomys kaiseri		2[1]			
Grammomys macmillani		2[1]		4	
Grammomys ibeanus	1		1		4[1]
Hylomyscus arcimontensis			3[1]	1	2
Lophuromys aquilus	2	1	2	3	4[1]
Praomys delectorum	3		3[1]	2	1
Graphiurus murinus				5	3
No. of species	3	3	5	5	5

[1] Rank shared by more than one species.

delectorum (38.1%); *H. arcimontensis*, (36.0%); *G. ibeanus* (10.2%); *L. aquilus* (9.5%); *Graphiurus murinus* (4.1%); and *B. hindei*, *Aethomys kaiseri*, and *Grammomys macmillani* (0.7% each). As in the East Usambara, relative abundance of each species varied among fragments (Table 7).

In general, *H. arcimontensis* and *P. delectorum* were captured in greater numbers than expected by chance (based on the assumption of equal distribution of individuals across all fragments) in the larger fragments, and both species of *Grammomys* were found in higher numbers in the smaller fragments. The capture rate of *Lophuromys* was also considerably higher in the smaller fragments and less than expected in the larger fragments in both mountain ranges.

Distribution of East and West Usambara Rodents Relative to Other Tanzanian Massifs

Three species of rodents were restricted to one of the Usambara massifs based on our trap line results: *Aethomys hindei* was trapped only in the West Usambara, and *Graphiurus kelleni* and the introduced *Rattus rattus* were only recorded from the East Usambara. All other rodent species documented during our study were found on both massifs. A finer level assessment of these taxa allow them to be divided into three groups: (1) widespread taxa that occur in disturbed open habitats, such as *Mastomys natalensis* and *Mus musculoides*; (2) species living in montane forest habitats across Tanzania regardless of the geological origin of the massif (Kilimanjaro, South Pare, West and East Usambaras, Nguu, Nguru, Ukaguru, Uluguru, Rubeho, Udzungwa, and Rungwe), such as *Grammomys ibeanus*, *Lophuromys aquilus*, and *Praomys delectorum*; and (3) species with similar distributions to group 2 and also forest dependent, but absent from younger northern volcanic mountains (Mts. Kilimanjaro and Meru), such as *Beamys hindei* and *Hylomyscus arcimontensis*. The distribution of *B. hindei* is notably broader than *H. arcimontensis*, as it also occurs in coastal forests to the east of the Usambaras (Stanley et al., 2005). Before human perturbation of natural forested habitats, the coastal formations were continuous with montane habitats of the East Usambara (Hawthorne, 1993), forming direct forested links for dispersal.

Differences between Rodent and Shrew Distributions

With few exceptions, the rodents found on the East and West Usambaras have widespread distributions across montane habitats of Tanzania. This pattern is in contrast to that of some of the forest-dwelling shrew species found on these two massifs, particularly *Crocidura tansaniana*, *C. usambarae*, and *Sylvisorex howelli*, which have very narrow ranges and are endemics or near endemics (Stanley et al., this volume a). Hence, shrews show a greater level of local endemism, compared with rodents, in the montane forest islands of Tanzania. Current taxonomy indicates *C. monax* to have the same distribution in Tanzania as *Praomys delectorum*, from Mt. Kilimanjaro to the Southern Highlands, but we suspect detailed morphological and molecular analyses of this shrew may reveal that it encompasses more than one species.

Elevational ranges of different taxa from each small mammal group, as currently circumscribed, such as *C. monax* and *P. delectorum*, offer insights into distributional patterns, in part overlaid on vegetational formations (Lovett & Pocs, 1993). Stanley et al. (2005) found *P. delectorum*, but not *C. monax*, at 230 m in the Kwamgumi Forest Reserve, composed of lowland forest habitat (Doggart et al., 1999) at the base of the East Usambara. On the Udzungwa massif, Stanley and Hutterer (2007) surveyed across an elevational transect of 600 (lowland evergreen forest) to 2000 m (montane and mountain bamboo forest; Shangali et al., 1998) and found the lower limit of *P. delectorum* documented during that study at 600 m and *C. monax* at 1460 m (montane forest). Thus, combining this information with data from the Usambara Mountains, *C. monax* appears to be restricted to montane formations at elevations of roughly 1000 m or higher, but *Praomys* occurs notably lower in drier habitats. Today, there is no continuous topographic or montane habitat connection among the different Eastern Arc Mountains and northern volcanoes at elevations greater than 1000 m and, thus, no dispersal corridors for montane forest-restricted taxa. Moreover, the vicissitudes of Quaternary climatic change and associated vegetational shifts may have had a less dramatic effect in the formation of dispersal corridors for montane-restricted taxa such as *C. monax*, which feed largely on invertebrates (Kingdon, 1974b), compared with more generalist seed-eating mammal species, such as *P. delectorum* (Genest-Villard, 1980).

Some lower elevation habitats in southern Tanzania (Lake Masoko, 9°20′S, 33°45′E, 770 m) likely contained open wet Zambezian woodlands during the past 4000 years, with at least three episodes of habitat transformation during this period, attributed to either natural climatic change, human-induced habitat alteration, or both (Vincens et al., 2003; Ryner et al.,

2006). However, there is no evidence that *P. delectorum* uses open lowland woodland habitat either currently or historically. For example, Fernández-Jalvo et al. (1998) found evidence of woodland habitat 1.7 mya in the Olduvai Gorge, but *Praomys* was not identified from the small mammal assemblages analyzed from that period.

Although riverine forest may be a potential dispersal conduit between some massifs today, faunal surveys give no evidence that *P. delectorum* currently occurs in this habitat; hence, it does not appear to use such corridors to disperse between different massifs with montane forest. For example, this species was trapped in the South Pare at 1100 m, but not in the Gonja Forest at 500 m. The two sites are separated by approximately 8 km but, until the recent past, were connected by forest along the Higilulu River (Stanley et al., 1998a, 2000).

We hypothesize that only when the forest type currently found on the mountains of Tanzania descended to lower elevations during natural Quaternary climatic shifts could taxa such as *P. delectorum* and *C. monax* disperse among different massifs. However, given the magnitude of these vegetational shifts and very different life history strategies between these two taxa, the capacity of *Praomys* to descend to lower elevations may have allowed dispersal across lower lying topographical bridges between mountains than the more parochial *C. monax*. Given their distributions and number of specimens available, these taxa are ideal candidates for morphological and molecular genetic analyses to test these hypotheses explicitly.

Seasonal Reproduction in Montane Tanzanian Rodents

Table 8 summarizes reproductive data for three rodent species (*Lophuromys aquilus*, *Hylomyscus arcimontensis*, and *Praomys delectorum*) for numerous sites in the Eastern Arc Mountains and nearby massifs. Previous work on this topic with rodents in the Eastern Arc Mountains includes that of Makundi (1995) and Makundi et al. (2006). These widespread taxa were the most commonly captured during field inventories conducted during the dry season (July–September) and allow examination of inter-annual, inter-habitat, and inter-site variation in certain reproductive parameters.

Lophuromys aquilus is strictly terrestrial and *H. arcimontensis* is arboreal. Although *P. jacksoni* has been documented to be partially arboreal (Kingdon, 1974a), we found *P. delectorum* to be primarily terrestrial in this study (Tables 9 and 10). These life history traits influence the formulation of hypotheses regarding possible seasonal effects on variation in the position of adult male testicles being scrotal or non-scrotal. To facilitate elevational comparisons for sites on different massifs, two separate elevational zones are presented in Table 8: ≤1300 m and >1300 m. We stress that the following observations are preliminary and require more study to be substantiated.

Inter-annual comparisons from the East and West Usambaras—A comparison of the reproductive data for these three rodent species in the East Usambara indicates that the sex ratio was relatively consistent among years and species, approaching parity, except *P. delectorum* in 1992, which was notably male-biased. For species with relatively large sample sizes during a given field season, there seems to be striking difference in the proportion of males with scrotal testes. The *L. aquilus* males were notably biased toward being non-scrotal. Very few of these non-scrotal individuals were sub-adult; hence, this skewed aspect is presumably related to seasonal reproduction. Further evidence of differences in annual reproductive seasonality can be gleaned from these data. For example, during the 1992 field season in the East Usambara, proportionately more male *H. arcimontensis* were scrotal than in *P. delectorum*, and in the former species, a greater percentage of the captured females were pregnant; this same pattern largely held for the 1993 season. The reproductive periods of these two species are apparently not synchronized.

Data on sex ratios of these rodents in the West Usambara during the three seasons shows some differences. Most notable was a female-skewed population of *H. arcimontensis* in 1992. Samples of *P. delectorum* were biased toward males in all three years, approaching and exceeding 2:1 in 1991 and 1993. Most male *H. arcimontensis* and *P. delectorum* were scrotal, but very few of the *L. aquilus* were. This is consistent with data of Makundi et al. (2006) in the Magamba Forest of the West Usambara, where seasonal variation in the latter species (noted in that paper as *L. flavopunctatus*) was found, with males being scrotal predominantly during March and April and December and January. This may imply remarkably short periods of male reproductive activity in this species and suggests an exceptional reproductive system (e.g., heavily biased polygamous reproductive strategies). For *P. delectorum* in the Magamba Forest, Makundi et al. (2006) noted that during July to September, males with abdominal testes were more common than scrotal males, but became less common between October and December. In our West Usambara samples in which $n > 4$, the number of pregnant females of these three taxa was notably low, not exceeding 9% of those examined specimens.

Inter-site and inter-habitat Comparisons from the East and West Usambaras—During each field season, our field inventories occurred during similar calendar periods in the East and West Usambaras; hence, the elevational range of sampled sites was a principal difference between these two massifs with regard to the reproductive condition of rodents. In the East Usambara, sites fell within the range 970 to 1150 m and, in the West Usambara, between 1170 and 1300 m (Stanley et al., this volume b). This allows for comparisons of the possible role of slight elevational differences in patterns of seasonal reproduction in these three rodent species.

For *L. aquilus*, the vast majority of males were abdominal across these two massifs and years and the sex ratio was notably close to one. Sample sizes for the percentage of pregnant females are insufficient to make meaningful comparisons. For *P. delectorum*, on both massifs, there was a greater proportion of males in the captured animals than females, and of these males, most were scrotal. Several possible explanations can be offered with regard to *P. delectorum* during the periods of our inventories: (1) males are reproductively active (with a higher proportion of scrotal testes); (2) males are defending territories (with a greater chance of being captured), although we have not found in the literature information on their reproductive ecology; and (3) males have greater home ranges, or at least are more active than females (with a greater chance of being captured). Where the data on the percentage of pregnant females in the sample are sufficient for interpretation, females in the East Usambara were more likely to be pregnant than in the West Usambara,

TABLE 8. Reproductive data for different populations of *Lophuromys*, *Hylomyscus*, and *Praomys* in the Eastern Arc Mountains and nearby massifs. All observations and measurements (in mm) were recorded between July and September, which is the dry season.

Survey	Species	Sex ratio M:F	Testes scrotal:abdominal Ratio	n	Testis length Mean ± SD	Range	n	Testis width Mean ± SD	Range	n	Pregnant %	n	Largest embryo size (mm) Mean ± SD	Range	n
Mountain (m)															
Kilimanjaro (2000–4000)	*Lophuromys aquilus*	37:30			14.2	12–16	16	9.1	7–12	16	20	15	25.7 ± 10.0	18–37	3
	Praomys delectorum	33:32	17:13	30	10.9 ± 3.1	4–18	23	6.2 ± 1.8	2–8	23	25	4	6		1
South Pare (1100)	*Hylomyscus arcimontensis*	0:1									0	1			
	Praomys delectorum	35:23	28:7	35	11.2 ± 3.4	3–15	29	6.3 ± 1.8	2–8	29	0	17			
South Pare (2000)	*Lophuromys aquilus*	4:1	0:4	4	10	10–10	2	6.5	6–7	2	0	1			
	Hylomyscus arcimontensis	5:7	5:0	5	12	11–13	2	7	7–7	2	50	4	14	12–16	2
	Praomys delectorum	26:24	24:2	26	12.0 ± 2.6	4–14	14	7.3 ± 1.6	2–9	14	0	12			
Udzungwa (600–910)	*Hylomyscus arcimontensis*	8:5	3:2	5	8.3 ± 3.9	4–12	4	5.0 ± 1.8	3–7	4	20	5	3		1
	Praomys delectorum	7:7	6:1	7	12.3 ± 0.6	12–13	3	7.3 ± 0.6	7–8	3	25	4	6		1
Udzungwa (1450–2000)	*Lophuromys aquilus*	34:27	1:24	25	11.5 ± 3.0	7–15	6	7.0 ± 2.2	4–10	6	0	9			
	Hylomyscus arcimontensis	7:9	5:1	6	10.4 ± 2.1	7–12	5	6.4 ± 1.1	5–8	5	0	6			
	Praomys delectorum	26:6	25:0	25	10.9 ± 1.2	9–14	17	6.9 ± 0.8	5–8	17	13	8	2		1
Ukaguru (1840–1900)	*Lophuromys aquilus*	16:24	0:7	7	12.8 ± 1.5	11–15	5	8.0 ± 0.7	7–9	5					
	Hylomyscus arcimontensis	4:8	4:0	4	13.0 ± 1.6	11–15	4	7.5 ± 1.0	7–9	4	60	5	6.8 ± 5.2	1.5–12	3
	Praomys delectorum	23:8	23:0	23	11.7 ± 1.6	9–14	16	7.1 ± 1.2	4–9	16	0	1			
Uluguru (1345–1850)	*Lophuromys aquilus*	11:10	1:8	9	10.6 ± 4.3	5–15	5	6.2 ± 2.7	2–8	5	0	1			
	Hylomyscus arcimontensis	11:19	7:3	10	12.2 ± 1.5	10–13	4	7.2 ± 0.9	6–8	4	20	10	9.5	9–10	2
	Praomys delectorum	45:30	30:12	42	12.6 ± 1.0	11–14	17	7.5 ± 0.7	6–9	17	67	9	10.8 ± 6.1	3–20	5
Rungwe (1870–2410)	*Lophuromys aquilus*	28:30	5:17	22	12.7 ± 2.1	10–17	12	8.1 ± 1.4	6–10	12	0	14			
	Hylomyscus arcimontensis	19:10	9:5	14	10.5 ± 3.6	5–15	13	5.8 ± 2.1	3–9	13	67	3	13	6–20	2
	Praomys delectorum	144:124	94:30	22	12.8 ± 2.8	4–17	66	7.5 ± 1.8	2–10	66	15	48	10.0 ± 5.2	6–20	6
Nguu (1180)	*Lophuromys aquilus*	16:8	0:5	5	6.6 ± 2.3	3–9	5	4.4 ± 1.7	2–6	5	0	5			
	Hylomyscus arcimontensis	0:1													
	Praomys delectorum	52:37	0:5	5	12.6 ± 1.7	8–16	27	7.3 ± 1.1	4–9	27	38	13	12.6 ± 6.5	3–21	5
Nguu (1430)	*Lophuromys aquilus*	10:7	0:10	10	11.0 ± 1.6	9–13	5	7.6 ± 1.5	6–10	5	0	0			
	Hylomyscus arcimontensis	1:1													
	Praomys delectorum	9:8	8:0	7	13.3 ± 1.2	11–15	7	7.4 ± 0.5	7–8	7	80	5	10.2 ± 8.6	2–20	4
Nguru (1000)	*Lophuromys aquilus*	2:2									0	1			
	Hylomyscus arcimontensis	1:1	1:0		15		1	7		1					
	Praomys delectorum	18:14	14:2	16	14.1 ± 1.1	12–15	10	7.1 ± 0.3	7–8	10	0	4			
Nguru (1500)	*Lophuromys aquilus*	5:3	0:3	3	12.5	12–13	2	7.0	7–7	2	33	3	18		1
	Hylomyscus arcimontensis	0:1													
	Praomys delectorum	11:6	11:0	11	12.6 ± 0.5	12–13	7	7.4 ± 0.5	7–8	7	0	4			
EU 1991	*Lophuromys aquilus*	5:3	1:2	3	13		1	9		1	100	1	9		1
	Hylomyscus arcimontensis	2:3	1:1	2							100	1	4		1
	Praomys delectorum	3:2	3:0	3	15		1	7		1	100	2	17.0	10–24	2
EU 1992	*Lophuromys aquilus*	50:43	23:24	47	9.3 ± 2.4	3–13	19	6.0 ± 1.5	2–8	19	18	17	31	30–32	2
	Hylomyscus arcimontensis	18:13	13:3	16	12.1 ± 4.6	3–17	14	6.3 ± 2.1	2–9	14	25	8	5	4–6	2
	Praomys delectorum	106:79	64:33	97	10.2 ± 3.7	3–15	61	5.6 ± 2.1	1–9	61	14	42	11.7 ± 6.2	6–22	6
EU 1993	*Lophuromys aquilus*	10:8	1:9	10	9.8 ± 1.8	7–11	5	6.6 ± 1.1	5–8	5	33	3	30		1
	Hylomyscus arcimontensis	3:6	3:0	3	14 ± 1.0	13–15	3	6.7 ± 0.6	6–7	3	50	4	4	3–5	2
	Praomys delectorum	30:24	22:5	27	12.7 ± 1.6	11–17	15	6.3 ± 1.5	3–8	15	8	12	11		1
WU 1991	*Lophuromys aquilus*	21:19	4:13	17	8.2 ± 2.9	6–13	5	4.8 ± 1.3	4–7	5	0	3			
	Hylomyscus arcimontensis	51:42	48:1	49	13.0 ± 2.7	7–17	26	6.5 ± 1.8	3–10	26	0	13			
	Praomys delectorum	51:23	37:12	49	12.0 ± 2.9	5–17	15	6.1 ± 1.6	2–8	15	0	7			

TABLE 8. *Continued.*

Survey	Species	Sex ratio M:F	Testes scrotal:abdominal Ratio	n	Testis length Range	n	Testis width Mean ± SD	Range	n	Pregnant %	n	Largest embryo size (mm) Mean ± SD	Range	n
WU 1992	*Lophuromys aquilus*	4:4	2:2	4	9–14	2	6.5 ± 0.7	6–7	2	50	2	3		1
	Hylomyscus arcimontensis	15:29	14:0	14	11–17	8	7.2 ± 1.2	6–9	8	0	15			
	Praomys delectorum	32:24	29:2	31	11–17	16	7.1 ± 1.0	6–9	16	9	11	5		1
WU 1993	*Lophuromys aquilus*	1:1	0:1	1										
	Hylomyscus arcimontensis	4:1	4:0	4	11–14	2	7.5	7–8	2	100	1	8		1
	Praomys delectorum	13:4	11:1	12	6–14	5	6.6 ± 2.1	3–8	5					
							11.5 ± 3.5							
							13.6 ± 1.9							
							13.7 ± 1.8							
							12.5							
							11.0 ± 3.3							

which might relate to elevation and seasonality of reproduction. In general, the same general patterns between the two massifs can be gleaned for *H. arcimontensis*. Most striking in this regard is the percentage of pregnant females between the two massifs. In 1992 and 1993 in the East Usambara, 25% (n = 8) and 50% (n = 4) of the females were pregnant; in 1992, 0% of 15 females were pregnant in the West Usambara.

INTER-HABITAT COMPARISONS FROM THE SOUTH PARE—The important elevational difference between the two South Pare sites, 1100 (surveyed in July 1993) and 2000 m (surveyed in August 1994; Stanley et al., 1996, 1998), also allow for consideration of the potential effect of elevation in reproductive seasonality. Comparable data and sample sizes from the two South Pare sites are only available for *P. delectorum*. At both 1100 and 2000 m, the sex ratio in this rodent was close to parity, but captured males were disproportionally skewed toward those with scrotal testes. Even though numerous females were dissected from these two elevational zones, no females were found with embryos. Hence, at this level of comparison, for two sites in montane forest separated by 900 m elevation, no important difference was found in aspects of reproduction in *P. delectorum*.

INTER-HABITAT COMPARISONS FROM UDZUNGWA—Lowland rainforest between 600 and 910 m and sub-montane forest to mountain bamboo forest between 1450 and 2000 m (Stanley & Hutterer, 2007) were surveyed between July and September 1995 in the Udzungwa. The ecological contrasts at these sites are notably more pronounced than those of the East and West Usambaras and the South Pare. Data are available from this massif for two taxa, *P. delectorum* and *H. arcimontensis*, but sample sizes in a few cases are not substantial.

Sex ratios at the lower sites approached one; at the higher zone, male *P. delectorum* were disproportionately represented. Consistent with other sites in the Eastern Arc and nearby mountains, (1) most males captured for both species were scrotal, particularly in *P. delectorum,* and (2) more females were pregnant in the lower elevational zone. This suggests that the reproductive season commences earlier or has a broader period in the lowland rainforest compared with the higher formations.

Rodent Species Previously Reported in the East and West Usambaras and Not Documented during This Study

Several rodent taxa that had been previously reported from the Usambara Mountains were not found in our 1991–1993 field studies, likely due to trapping methodologies. *Otomys sungae* Bohmann, 1943, has been collected in the West Usambara in the Magamba Forest at 1585 m (Musser & Carleton, 2005; specimens in FMNH). As a strict herbivore, *Otomys* is not commonly attracted to our traps baited with coconut and peanut butter. However, *O. sungae* may occur in an elevational zone higher than that we sampled, which was below 1300 m.

Makundi et al. (2003) collected *Arvicanthis nairobe* J. A. Allen, 1909 from Shume Ward (4°42′16″S, 38°12′16″E, above 1800 m) in the West Usambara. This species was captured in traps baited with peanut butter mixed with maize bran in both fallow land and forest. Although the absence of this species from our study sites may be associated with a higher elevational range than that of our study, it occurs in dry habitats at approximately 1000 m in Tarangire National Park

TABLE 9. Microhabitat occurrences of rodent species by fragment size in the East Usambara Mountain in 1992. Data for the control area come from trap lines AF, AG, and AI only (Stanley et al., this volume a). Explanations for information on trap placements are keyed to numerical notes presented at foot of table.

Fragment size and rodent species	No. trapped	Trap position			Ground location[1]					Above ground location[2]		
			Above ground									
		On ground	≤1 m above ground	>1 m above ground	Leaf litter, 1	Herbaceous vegetation, 2	Under or near rotten wood, 3	By roots, trunks, fresh logs, 4	Misc., 5	Vine, limb or trunk <10 cm, 6	Vine, limb or trunk >10 cm, 7	Misc., 8
1–10 ha												
Trap distribution		240	48	83	19	35	34	75	77	81	7	43
Beamys	1			1								1
Lophuromys	33	32	1			8	3	14	7	1		
Grammomys ibeanus	1		1									1
Grammomys macmillani	10	6	1	3		1		3	2	2		2
Praomys	40	38	2		1	3	3	10	21	2		
29.4 ha												
Trap distribution		70	8	12	14		19	25	12	15	1	4
Lophuromys	5	5					2	3				
Hylomyscus	1			1						1		
Praomys	13	12	1		6		1	1	4	1		
Rattus	1	1							1			
Control												
Trap distribution		154	28	42	22	6	30	58	38	49	6	15
Beamys	3	2		1				2		1		
Lophuromys	5	5					1	2	3			
Hylomyscus	16	10	2	4	1			5	4	4	1	1
Mastomys	1	1							1			
Praomys	44	37	5	2	3	3	15	6	10	3	1	3
Graphiurus	2	2						2				

[1] **On ground**: (1) In area of open understory; (2) in thick herbaceous vegetation; (3) under or near (<30 cm away) highly decomposed logs or stumps; (4) under or near living or recently fallen tree parts, including roots, trunks, and logs; (5) miscellaneous, including on muddy stream banks and in, under, or near (<30 cm away) large rocks or rock piles (both exposed or covered with moss).

[2] **Above ground**: (6) On vines, limbs, or trunks less than 10 cm in diameter regardless of orientation; (7) on limbs or trunks greater than 10 cm in diameter; (8) miscellaneous settings.

(Stanley et al., 2007c), and may have recently colonized the Shume area.

Acomys ignitus Dollman, 1910, has been noted in the literature as occurring in the "Usambara Mountains" (e.g., Musser & Carleton, 2005), and this species has been referred to as a "near endemic" to the Usambara massifs (Burgess et al., 1998). The type locality of *A. ignitus* is Voi, Kenya, but little is known about its distributional range. J. T. Zimmer collected two specimens referable to this species in 1926. The first (FMNH 27295) was obtained near Lake Manka at approximately 435 m. Other mammals from the same collection and locality include the gazelle *Litocranius walleri*, a distinctly dry habitat animal. The second *A. ignitus* (FMNH 27296) was collected near Mnazi, at approximately 600 m and adjacent to drier habitats. Both sites are lowland dry habitats, and it is inappropriate for *A. ignitus* to be listed among the montane mammals of the Usambaras or to be considered endemic or near-endemic to these massifs.

Cricetomys ansorgei Thomas, 1904, was documented by Cordeiro et al. (2009; as *C. gambianus* Waterhouse, 1840) in the forests of the Amani area, and we found traps set by local residents for this large rodent in the West Usambara 37.8-ha fragment. Although *Rattus rattus* was found during our study, other commensals, such as *Mus musculus* Linnaeus, 1758, were not. Given that most of our trapping was away from human habitation, it is not surprising that these two species were rare or absent in our captures.

Conclusions

The rodent fauna of the East and West Usambara Mountains is diverse and remains poorly studied. In particular, we know little about historical shifts in rodent species and elevational distribution as a function of human-induced habitat alteration. This has important bearing, for example, associated with the range of *Mastomys* and its ectoparasites, which are reservoirs of bubonic plague in the West Usambara (Kilonzo et al., 1997). Furthermore, certain rodent species are presumed to be important dispersers of seeds and fruits. Hence, they likely play an important role in tree regeneration and, by extrapolation, the integrity of the forest ecosystem. Additional field surveys and associated morphological and molecular genetic analyses are needed to place the rodent fauna of the Usambara massifs in a broader perspective with regards to other mountain complexes in the eastern portion of Africa and should provide further insight into the reproductive systems and aspects of seasonality in these animals.

TABLE 10. Microhabitat occurrences of rodent species by fragment size in the West Usambara Mountains in 1991. Data for the control area come from trap lines A and B only (see Stanley et al., this volume a). Explanations for information on trap placements are keyed to numerical notes presented at foot of table.

Fragment size and species	No. taken	Trap position: On Ground	Trap position: Above ground: ≤1 m above ground, A	Trap position: Above ground: >1 m above ground, B	Ground location[1]: Leaf litter, 1	Ground location[1]: Herbaceous vegetation, 2	Ground location[1]: Under or near rotten wood, 3	Ground location[1]: By roots, trunks, fresh logs, 4	Ground location[1]: Misc., 5	Above ground location[2]: Vine, limb, or trunk <10 cm, 6	Above ground location[2]: Vine, limb, or trunk >10 cm, 7	Above ground location[2]: Misc., 8
1–10 ha												
Trap distribution		65	19	26	21	17	8	13	6	28	13	4
Aethomys	1	1			1							
Beamys	1	1				1						
Lophuromys	7	7				5	1		1			
Grammomys ibeanus	10		1	9						8	2	
Grammomys macmillani	1		1							1		
Hylomyscus	1			1						1		
Praomys	3	3			1		2					
37.8 ha												
Trap distribution		66	20	14	3	7	10	22	24	17	11	6
Lophuromys	5	5				4			1			
Grammomys ibeanus	3		3						3			
Hylomyscus	18	8	3	7		2		2	4	8	2	
Praomys	7	7				1	1	1	4			
Graphiurus	2	1	1						1		1	
Control												
Trap distribution		150	22	28	6	3	34	56	51	26	17	7
Lophuromys	2	2			1			1				
Grammomys ibeanus	2	2			1		1					
Hylomyscus	34	12	5	17	1		1	4	6	13	3	6
Praomys	46	36	6	4	2		11	11	12	4	4	2
Graphiurus	4	2	1	1				2		1	1	

[1] **On ground**: (1) In area of open understory; (2) in thick herbaceous vegetation; (3) under or near (<30 cm away) highly decomposed logs or stumps; (4) under or near living or recently fallen tree parts, including roots, trunks, and logs; (5) miscellaneous, including on muddy stream banks and in, under, or near (<30 cm away) large rocks or rock piles (both exposed or covered with moss).

[2] **Above ground**: (6) On vines, limbs, or trunks less than 10 cm in diameter regardless of orientation; (7) on limbs or trunks greater than 10 cm in diameter; (8) miscellaneous settings.

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Chapter 5

Herpetofauna of Montane Areas of Tanzania. 1. Results from Two Amphibian Surveys of Malundwe Mountain, Mikumi National Park

Lucinda P. Lawson[1] and Leah Collett[2]

[1] *USDA-ARS-CMAVE, 1600 S.W. 23rd Drive, Gainesville, FL 32608, USA*
[2] *Animal & Environmental Research Group, Department Life Sciences, Anglia Ruskin University, East Road Cambridge UK CB1 1PT*

Abstract

As part of a larger survey of flora and fauna of Malundwe, funded by Critical Ecosystems Partnership Fund, amphibians were collected on three separate surveys of this mountain between 2004 and 2007. These surveys constitute the first surveys for amphibians in this part of the Eastern Arc Mountains, a global biodiversity hotspot. Samples from these surveys revealed an amphibian fauna with links to the rest of the Eastern Arc Mountains. Only relatively few species were found during these surveys, probably due to a small cumulative sampling effort, lack of a permanent water source, and the very small size of this forest fragment. The amphibian fauna of Malundwe shares an affinity with the Uluguru Mountains, both in terms of species composition of each mountain block and genetic proximity for species with available population level data. I describe the species and associated microhabitat from the available voucher specimens resulting from the Malundwe surveys.

Introduction

Malundwe Mountain is a little-known and often overlooked massif of the Eastern Arc Mountain (EAM) chain in Tanzania. With a total forested area of only 4.5 km^2, this section of afromontane rainforest is one of the smallest blocks in the chain, and one of only two protected by Tanzania National Parks (TANAPA) (Lovett & Norton, 1989; Stanley et al., 2005). Recent surveys, funded through the Critical Ecosystems Partnership Fund (CEPF), have helped to document the floral and faunal diversity of this series of peaks and to explore the relationship to other mountain ranges in close proximity (e.g., the Uluguru and Udzungwa Mountains). This study constitutes the first survey of amphibians in this Eastern Arc Mountain fragment and, given the pattern of endemism in the region (Poynton et al., 2007; Blackburn, 2009; Blackburn & Measey, 2009), is an important contribution to our understanding of amphibians in this global biodiversity hotspot (Myers et al., 2000).

Study Area

Malundwe Mountain is located approximately 300 km west of Dar es Salaam in southern Mikumi National Park (MNP) (7°24′S, 37°18′E; Fig. 1) in central/eastern Tanzania. The three peaks that make up this small range reach a maximum height of 1250 m elevation, with afromontane forests extending from the peak down to 800–900 m on the eastern slopes (Lovett & Norton, 1989). The total amount of forested area, divided between two patches, is 4.5 km^2, with a closed forest canopy height of 20–30 m (Lovett & Norton, 1989). Along with the Taita Hills, this total forest area comprises one of the smallest patches of forest in the entire Eastern Arc (Newmark, 2002; Burgess et al., 2007). Malundwe is unique, however, in that the entire area of mid-elevation forest is naturally very small (unlike the Taita Hills, where deforestation is a major factor in the small area of extant forest) and has been isolated and protected in the middle of a large area of preserved savannah, likely never affected by human encroachment. There is only one source of groundwater among these peaks: a small stream flowing adjacent to the research camp area established for biodiversity surveys (Fig. 1) (7°23.719′S, 37°18.279′E, 985 m) (Stanley et al., 2007). This stream can also be encountered farther down the slope as a slow-moving stream/wetland near the base camp (7°21.913′S, 37°17.338′E, 840 m) (Stanley et al., 2007). The water source is not permanent and is often completely dry by August until the rainy season beginning in December (observation by Animal Behaviour Research Unit research team (ABRU), Mikumi National Park).

Surveys

The amphibians collected during survey work in 2007 were incidentally encountered during small mammal surveys through digging of pitfall lines (see Chapter 1 of this volume),

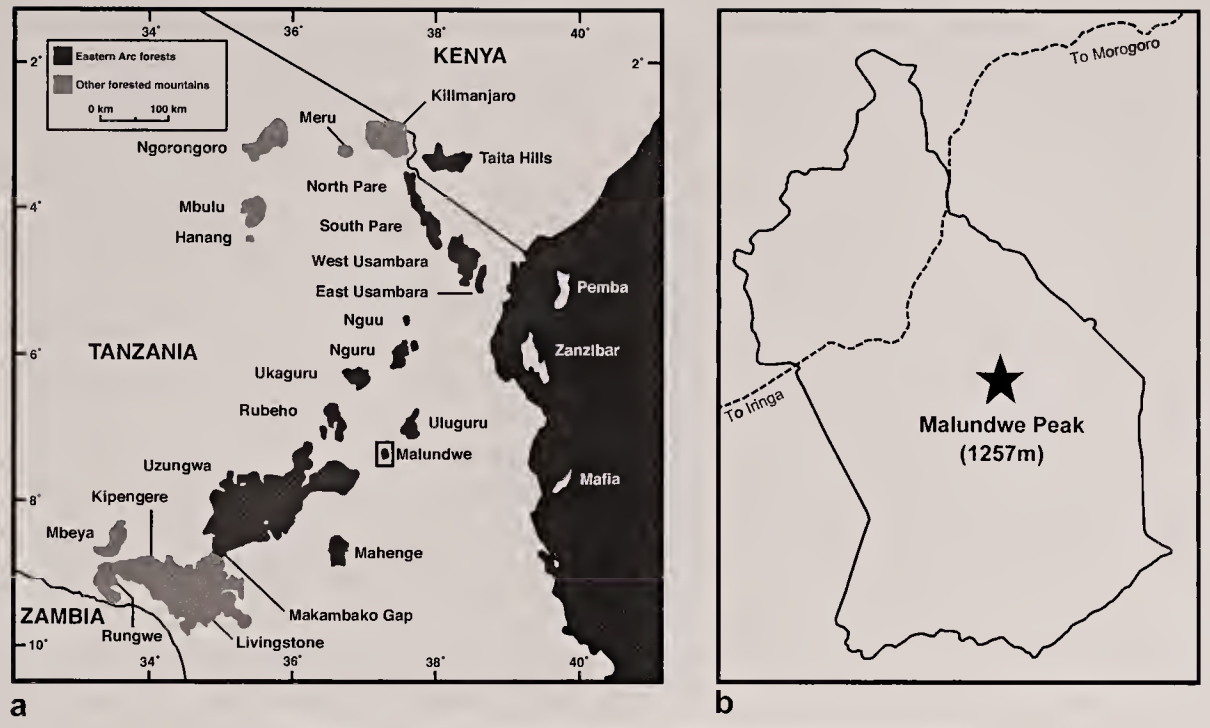

FIG. 1. Maps of the Eastern Arc Mountains with Malundwe boxed (**a**) and in Mikumi National Park in Tanzania (**b**); elevational map of Malundwe peak showing research camps (**c**). Figure created by Rebecca Banasiak and used with permission from Stanley et al. 2005.

collected in pitfall lines, and through chance encounters while walking. An additional incidental survey took place in 2004, but the material appears to have been lost. In contrast, in 2006, an effort was made to survey specifically for the herpetofauna of this region by including a herpetologist (Lawson) in the survey team. The 2005 survey was conducted in July (dry season) over a 10-day period (2005), with no concentrated effort collecting amphibians. The survey in 2006 was conducted over a seven-day period in early May (rainy season) with a distinct goal of cataloguing amphibians. The survey team followed the route of Stanley et al. (2007) to reach the Malundwe research camp with one night at the beginning of the survey and one night at the end of the survey at a base camp at the edge of the forested peaks (7°21.913′S, 37°17.338′E, 840 m), where we searched for amphibians in the evenings. We spent six nights at the research camp searching for amphibians night and day (7°23.719′S, 37°18.279′E, 985 m).

Methods

During the 2005 survey, caecilians and frogs were collected that were either recovered while installing pitfall buckets, caught in pitfall lines, or encountered while walking through the forest during the day. Herpetological surveys in 2006 were conducted primarily in areas within 200 m of water and extending along crests in the hills through pitfall lines. Each day, researchers searched for frogs among the leaf litter, on trees or other vegetation, and in the pitfall buckets. At night, researchers again searched leaf litter, trees, and low vegetation near water sources. Whenever possible, call recordings were made during the 2006 foray with a Marantz PMD660 Digital Recorder and linked to the associated specimen (FMNH collection). For processing specimens, each individual was first photographed and euthanized with MS222. Tissues were then taken from the liver and inner thigh and stored in DMSO buffer for molecular analysis. Specimens were then preserved

in formalin (10%), rinsed in water, and stored in ethanol (70%) for morphological analysis. Standard external measurements were taken for each specimen. Each specimen was assigned a field number based on the collector (Leah C. Collett, LCC; Lucinda Lawson, LL; Kate B. McQuaid, KBM; David C. Moyer, DCM; William T. Stanley, WTS). Specimens are currently deposited at the Field Museum of Natural History, Chicago (FMNH); the Natural History Museum, London (BMNH); and the Museo Tridentino di Scienze Naturali, Trento, Italy (MTSN). Specimens listed as "cf." indicate that the taxon shares an affinity with a known species, but slight morphological variation questions a definitive ID. Further morphological and molecular investigations are being conducted, and full species descriptions will be published following these studies.

Results

The incidental amphibian encounters of 2005 and 2007 yielded 13 anurans and two caecilian specimens, all from the research camp area (higher elevation). The species found in this survey are: *Arthroleptis* cf. *affinis, A. stenodactylus, A. xenodactyloides, Probreviceps* cf. *macrodactylus, Scolecomorphus* cf. *vittatus*, and *Boulengerula* cf. *uluguruensis.*

The week-long survey of 2006 encountered a total of 34 amphibians. At the base camp (lower elevation), we encountered *Afrixalus fornasini, A. stuhlmanni, Arthroleptis stenodactylus, Hyperolius puncticulatus, Ptychadena oxyrhynchus,* and *Ptychadena* sp. At the research camp, we encountered *Arthroleptis* cf. *affinis, A. stenodactylus, A. xenodactyloides, Leptopelis uluguruensis, Nectophrynoides* cf. *tornieri, Boulengerula* cf. *uluguruensis*, and *Scolecomorphus* cf. *vittatus.*

Annotated List of Amphibians Collected from Malundwe Mountain

Voucher specimens are referred to by Museum accession numbers where available and field numbers (e.g., WTS, LCC) for those yet to be accessioned at the Natural History Museum (NHM), London.

Anurans

***Afrixalus fornasini* (Bianconi, 1849)**

The individual found possesses the dorsal color pattern of broad light bands from the nostrils to the urostyle separated by a thick, dark central band. Sides and feet are dark brown. The specimen is a large female with large, conspicuous, black-tipped asperities on head, back, and the dorsal surfaces of limbs. These characteristics, along with the tibia/snout–urostyle length (SUL) ratio of this specimen (45%), correspond with Pickersgill's (2007) description. The head width/tibia ratio, however, is much higher than his description (106% instead of the 51%–80% ratio described). The dorsal pattern of this individual clearly most closely resembles photos depicting *A. fornasini* as opposed to *A. unicolor* in Pickersgill (2007), which Pickersgill considers to be potentially a separate species. Further molecular work will be necessary to determine whether these are different species and, if so, which of the two species this individual belongs to (Poynton, 1964; Schiøtz, 1975; Poynton & Broadley, 1987b; Schiøtz, 1999).

Specimens Examined—FMNH 275600.

***Afrixalus stuhlmanni* (Pfeffer, 1893)**

Individuals have the typical dorsal pattern described for this species, a pair of slightly convergent dark lines from the rump over the back to between the eyes, with a scattered distribution of asperities (Schiøtz, 1974; Poynton & Broadley, 1987a; Pickersgill, 2005; Poynton, 2006).

Specimens Examined—FMNH 275602–275607.

***Arthroleptis* cf. *affinis* (Ahl, 1939)**

Based on morphological measurements, the individuals from this survey fall well within the characteristics of *A. affinis* outlined by Poynton and Loader (2008). Head width/SUL ratios for individuals from this collection ranged from 38.3%–45.2%, within the ranges (34.8%–45.9%) given by Poynton and Loader (2008). Additionally, inner metatarsal tubercle/head width ratios ranged from 11.3%–14.2%, most of which were in the known range of *A. affinis* of 8.70%–13.77%. The highest ratio (14.2%) is from a poorly preserved specimen (making it difficult to measure the tubercle), and if exeluded, these frogs have a range from 11.3%–12.6%. Molecular data show this population to be closely associated to Uluguru populations (Channing, 2001; Channing & Howell, 2006; Blackburn, 2008; Poynton & Loader, 2008).

Specimens Examined—FMNH 272056; WTS 6768, 6795, 6820, 6832; LCC 009.

***Arthroleptis stenodactylus* (Pfeffer 1893)**

Specimens have the heavily built body with relatively short rear legs characteristic of this species (Poynton & Loader, 2008). Inner metatarsal tubercles are distinct and shovel shaped (Poynton, 1964; Poynton & Broadley, 1985; Channing, 2001; Channing & Howell, 2006).

Specimens Examined—FMNH 272054, 272055, 275599; LCC 011, 013; WTS 6850.

***Arthroleptis xenodactyloides* (Hewitt 1933)**

Adults from this collection range in size from 12.95 to 19.10 mm. Dorsal coloration on some individuals is mottled brown with banded arms and legs. Ventral surface of limbs and throat are gray/pink. Ventral surface is white/gold. Digits have small distinct discs in a teardrop shape, and hands and feet are marked with many tubereles (Poynton, 1964; Poynton & Broadley, 1985; Channing, 2001; Channing & Howell, 2006).

Specimens Examined—WTS 6802, 6764–6756; FMNH 272057.

***Hyperolius puncticulatus* (Pfeffer 1893)**

Although the pattern in *H. puncticulatus* can be variable, the Malundwe population appears solely to exhibit the most common color morph: yellow dorsum with conspicuous black-lined canthal and dorsolateral stripes (Schiøtz, 1975; Poynton & Broadley, 1987c; Schiøtz, 1999).

Specimens Examined—FMNH 274351–274359.

Leptopelis uluguruensis **(Barbour and Loveridge 1928)**

Dorsal coloration of these individuals ranged from a brown-green background at night to blue-green during the day, mottled with small yellow spots. Individuals possess red-gold pupils/iris. The ventral surface is white with very blue points at shoulder joints, waist, and knee and ankle joints. The heads are characteristic of the species, with a broad shape and short nose (Schiøtz, 1975, 1999).

Specimens Examined—FMNH 275626–275628.

Nectophrynoides **cf.** *tornieri* **(Roux 1906)**

The dorsal coloration of this individual is mottled black/brown, with dark sides. Legs, feet, toes, and thighs are speckled. Ventral side is dark and flecked with white dots. The throat of this individual is pale grey with white flecks. Groin and toes are pink. Eyes are golden. The head is thick at the base (spade shaped), and the back and legs are covered in small warts (Roux, 1906; Channing, 2001; Menegon et al., 2004; Channing & Howell, 2006). The taxonomic status of this individual is currently being assessed by M. Menegon and S. P. Loader.

Specimens examined—MTSN 7329.

Probreviceps **cf.** *macrodactylus* **(Nieden, 1926)**

This is a juvenile specimen in which a tympanum is visible. Juveniles of the subspecies *P. macrodactylus* and *P. loveridgei* are difficult to distinguish; thus, further surveys are needed.

Specimens Examined—LCC 010.

Ptychadena oxyrhynchus **(Smith 1849)**

Although this specimen (and potentially the unknown *Ptychedena* sp. listed below) appears to have not reached adult size, it is identifiable based on morphological characteristics outlined in Channing (2001), Channing and Howell (2006), and Pickersgill (2007). This specimen has several dorsolateral ridges, and as fitting with the description of the species, the two median ridges begin at the posterior of the eye and end in the middle of the back. Distal to these medial ridges, two other ridges extend from behind the eyes and continue to the vent. The tympanum (typ) is clearly visible, and it reaches almost the eye diameter (typ/eye = 0.88, in line with the described range of 0.8–1.0). The hind legs are long and muscular as described for the species; the ratio of femur/SUL is 57%. The tibia/SUL ratio is also slightly small, 63% as opposed to 0.7–0.8 (Channing 2001), or 67%–77% (Pickersgill 2007). Foot and longest toe measurements, however, are slightly high (0.92) for the range (0.8–0.9). Toe-tips and finger-tips are not enlarged. Eye diameter = 4.69 mm, tympanum width = 4.12 mm (tympanum height = 3.5 mm). Femur = 22.2 mm, tibia = 24.6 mm, foot = 35.77 mm, inner metatarsal = 3.00 mm. The distance from the nostrils to the snout is approximately equal to the internarial distance. This specimen is dark green/brown with gold ridges down the back. Speckled brown/cream sides. The upper section of the iris is golden, throat and dorsal surfaces white. Underside of thighs pinkish with cream spots. Back of thigh had light and dark longitudinal bands (Schmidt & Inger, 1959; Poynton, 1964; Inger, 1968; Channing, 2001; Channing & Howell, 2006; Pickersgill, 2007).

Specimens Examined—FMNH 275593.

A second possible *P. oxyrhynchus* specimen was also found, although as a juvenile, the identity is uncertain. The specimen has a long snout and three horizontal bands on the back of the thighs connecting the knees.

Specimens Examined—FMNH 275601.

Gymnophiona

Boulengerula **cf.** *uluguruensis* **(Barbour & Loveridge 1935)**

The specimens closely match the description of *Boulengerula uluguruensis* by Nussbaum and Hinkel (1994), particularly in the coloration and annuli counts. Furthermore, Loader et al. (in press) indicate a close phylogenetic relationship between Uluguru populations of *B. uluguruensis* to Malundwe, although there is substantial genetic difference between these populations.

Specimens Examined—LCC 003; KBM 003. These are in the process of being accessioned into the BMNH collection.

Scolecomorphus **cf.** *vittatus* **(Boulenger 1895)**

Three of the four specimens found for this species have annuli counts within the regular range for this species (130, 133, and 136). The fourth specimen (KBM 005) extends the variation of number annuli for this species to 150 (148 was the previous maximum known). The coloration of the specimens resembles that of Nussbaum's (1985) description of *S. vittatus* (Loader et al., 2003a,b; Gower et al., 2004).

Specimens Examined—LCC 004; KBM 002. 004. 005. These are in the process of being accessioned into the BMNH collection.

Discussion

Although this is only the first, and relatively preliminary, investigation of the amphibians of Malundwe, the collection offers a glimpse of the diversity in this poorly known Eastern Arc forest fragment. The small isolated peaks of the Malundwe range contain a small subset of the known amphibian diversity of larger Eastern Arc Mountains (Table 1). This reduced biodiversity may be a result of the small size of this fragment, which is a fraction of the size of most others in this system. For example, Malundwe has a total forested area of 4.5 km^2, whereas the other mountains, although heavily deforested in many cases, are hundreds of square kilometers. Pare Mountains have 484 km^2 of forest, West Usambara 328 km^2, East Usambara 413 km^2, Nguru 647 km^2 including Nguu, Ukaguru 184 km^2, Uluguru 527 km^2, Rubeho 499 km^2, Udzungwa 1960 km^2, and Mahenge 291 km^2 (Newmark, 1998). The Taita Hills are the only comparable area with just 6 km^2 of forest, although the original amount was much greater. In comparing Malundwe species diversity to lists from the Udzungwa, Uluguru (Malundwe's nearest neighbor), and the East Usambara Mountains, it is apparent that the species encountered at Malundwe appear to be the omnipresent types, found on many mountain areas throughout the EAM. When species are shared between a subset of mountains and Malundwe, those on Malundwe appear to be more similar to the northern localities (the Uluguru Mountains and the East Usambara) than the southern locality (Udzungwa). Based on molecular datasets, preliminary work on *Boulengerula uluguruensis* and *Hyperolius puncticulatus* suggests that Malundwe populations show the closest phylo-

TABLE 1. Comparison of amphibians encountered on Malundwe Mountain and lists compiled from the literature and chapters in this edited volume from the East Usambara, Uluguru, and Udzungwa Mountains.

	Udzungwa	Malundwe	East Usambara	Uluguru
Anura				
Afrixalus brachycnemis	x		x	x
Afrixalus delicatus	x			x
Afrixalus fornasini	x	x	x	x
Afrixalus morerei	x			
Afrixalus stuhlmanni		x	x	x
Afrixalus uluguruensis	x		x	x
Amietia angolensis	x		x	x
Amietophrynus gutturalis	x		x	x
Amietophrynus maculatus	x		x	x
Arthroleptides martiensseni			x	
Arthroleptis affinis	x	x	x	x
Arthroleptis reichei	x			
Arthroleptis stenodactylus	x	x	x	x
Arthroleptis xenodactyloides	x	x	x	x
Arthroleptis xenodactylus			x	
Arthroleptides yakusini	x			x
Breviceps mossambicus	x		x	
Bufo brauni	x		x	x
Bufo lindneri	x			
Callulina kreffti	x		x	x
Chiromantis xerampelina	x		x	x
Hemisus marmoratus	x		x	
Hildebrandtia ornata	x			
Hoplophryne rogersi			x	
Hoplophryne uluguruensis	x			x
Hyperolius argus			x	
Hyperolius kihangensis	x			
Hyperolius minutisimus	x			
Hyperolius mitchelli	x		x	x
Hyperolius parkeri	x		x	
Hyperolius pictus	x			
Hyperolius puncticulatus	x	x	x	x
Hyperolius spinigularis			x	x
Hyperolius tuberilinguis	x		x	
Hyperolius mariae			x	
Kassina maculata	x		x	
Kassina senegalensis	x		x	
Leptopelis barbouri	x		x	
Leptopelis flavomaculatus	x		x	x
Leptopelis parkeri	x		x	x
Leptopelis uluguruensis	x	x	x	x
Leptopelis vermiculatus	x		x	
Mertensophryne micranotis			x	x
Nectophrynoides asperginis	x			
Nectophrynoides cryptus				x
Nectophrynoides frontierei			x	
Nectophrynoides laevis				x
Nectophrynoides minutus				x
Nectophrynoides poyntoni	x			
Nectophrynoides pseudotornieri				x
Nectophrynoides tornieri	x	x	x	x
Nectophrynoides viviparus	x			x
Nectophrynoides wendyae	x			
Parhoplophryne usambarica			x	
Phrynobatrachus acridoides	x		x	x
Phrynobatrachus kreffti			x	
Phrynobatrachus mababiensis	x			
Phrynobatrachus natalensis	x			x
Phrynobatrachus parvulus	x			
Phrynobatrachus rungwensis	x			
Phrynobatrachus uzungwensis	x			x
Probreviceps macrodactylus	x		x	x
Probreviceps rungwensis	x			
Probreviceps uluguruensis				x
Ptychadena anchietae	x		x	
Ptychadena grandisonae	x			
Ptychadena mascareniensis			x	
Ptychadena mossambica	x			
Ptychadena oxyrhynchus		x	x	x
Ptychadena porosissima	x			

TABLE 1. *Continued.*

	Udzungwa	Malundwe	East Usambara	Uluguru
Ptychadena taenioscelis	x			
Ptychadena uzungwensis	x			
Pyxicephalus edulis	x			
Schismaderma carens	x		x	
Spelaeophryne methneri	x			x
Stephopaedes usambarae			x	
Strongylopus fuelleborni	x			
Xenopus laevis	x		x	x
Xenopus mulleri			x	
Xenopus cf. *petersii*	x			
Gymnophiona				
Scolecomorphus vittatus		x	x	x
Boulengerula ulugurensis		x		x
Boulengerula boulengeri			x	
Scolecomorphus kirkii	x			x
Scolecomorphus uluguruensis				x

genetic relationships to Uluguru populations (Lawson, 2010; Loader et al., in press). The similarity of the overall amphibian communities and the low genetic diversity between populations of species on Malundwe and the Uluguru Mountains indicate that these forest fragments are among some of the more closely related but separated areas within the Eastern Arc system (Loader et al., 2004; Poynton et al., 2007; M. Menegon, unpubl. data). Unfortunately, species lists throughout the Eastern Arc are too incomplete and mountain ranges too unevenly sampled to make broad comparisons of assemblages (Poynton et al., 2007).

The Malundwe block is one of the smallest of the Eastern Arc blocks and has been found to be completely without water during the dry season (L. Collett, pers. com.: dry season foray by ABRU team, 2004). Both the small total forest area and the potential vulnerability of the area to drought might mean that amphibian populations in Malundwe may not be stable through time, possibly acting as a metapopulation sink with the genetically and spatially proximal Uluguru Mountains. The description of the Malundwe Mountain amphibians fills a gap in our understanding of endemism and species distributions throughout the Eastern Arc, addressing connectivity between northern and southern mountain populations. With focused sampling effort, the biogeographical connections of Malundwe with the other Eastern Arc fragments and the distinctiveness of its amphibian assemblage will aid biologists and conservationists in understanding the diversity within this dynamic area. Although, at present, Malundwe appears to only have widespread species, a closer examination may reveal some of those to be specifically distinct from other EAM species and endemic to Malundwe.

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Chapter 6

Herpetofauna of Montane Areas of Tanzania. 2. Altitudinal Distribution of Amphibians on the Uluguru South Mountains

Wilirk Ngalason[1] and Felix J. Mkonyi[2]

[1]*Department of Zoology and Wildlife Conservation, University of Dar es Salaam, P.O. Box 35064, Dar es Salaam, Tanzania*
[2]*Department of Biological Sciences, Dar es Salaam University College of Education, P.O. Box 2329, Dar es Salaam, Tanzania*

Abstract

We present data on the altitudinal distribution of amphibians on the western slopes of Uluguru South Mountains, Tanzania. These mountains form part of the Eastern Arc Mountains, which are known for their biodiversity richness. We used drift fences with pitfall buckets, plots, and audio-visual survey methods. A total of 21 species was found during the survey. Four species previously reported in the Uluguru South Mountains were not found during the present survey. Generally, the number of species was highest at lower altitudes and decreased with increased altitude. Species similarity index showed that the study sites adjacent to each other had greater similarity in amphibian species composition than did sites distant from each other. The Uluguru Mountains are characterized by altitudinal variation in vegetation types and climatic factors such as temperature and rainfall, which may affect the distribution of amphibians on the mountain.

Introduction

The distribution of animal species largely relates to their habitat requirements. The primary environmental factors that limit the distribution of species include climate, topography, vegetation type, microhabitat, soil, and geology (Davis et al., 1990; Heyer et al., 1994). Linked to changes in environmental factors is altitude, and this parameter is often used for examining the distribution and richness of species across habitats. Changes in the richness of amphibians across altitudinal gradients have been examined across the globe (e.g., Fauth et al., 1989; Owen, 1989; Buckley & Jetz, 2007). Declines in amphibian diversity with increases in altitude correspond to changes in environmental factors, wherein areas with less favorable conditions support fewer species (Poynton, 1962).

Generally, the distribution of amphibians along an altitudinal gradient is not uniform (Brown & Alcala, 1961; Scott, 1976; Heatwole, 1982). There appear to be some discrete "cut-off points" at which the lowland species are separated from those in the upland areas. Studies of southern and East African lowland and mountain systems have shown species turnover, changing between different areas with climatic variations that determine these cut-off points (Poynton, 1990, 1992, 2000, 2003; Loader et al., 2004).

The Uluguru Mountains form part of the Eastern Arc Mountains, which are a chain of isolated crystalline mountains running from southern Kenya through Tanzania in a crescent-shaped arc (Lovett, 1990). The Eastern Arc Mountains form one of the global biodiversity hotspots due to their high species diversity (Myers et al., 2000), a consequence of factors including fragmentation associated with altitude, zonation of climate, and altitudinal turnover in species composition (Poynton et al., 2006). The Uluguru Mountains are divided into Uluguru North and Uluguru South. They rise to about 2600 m above sea level on the Lukwangule Plateau. The lower slopes, from 600 to about 1600 m, have been deforested, whereas the mid-altitude portions are still covered by degraded forest. The only intact portion is located on the higher altitudes above 2000 m. Annual distribution of rainfall and dry season length are the main climatic factors determining forest limits in the Eastern Arc Mountains, with the exception of frost, which determines the upper altitudinal limits (Lovett, 1993). Forests in the Uluguru Mountains are divided into lowland (below 500 m), submontane (800–1500 m), montane (1500–1850 m), and upper montane forest (1850–2400 m) (Pócs, 1976a, b, c). Above the forest limits are heath and grassland vegetation on the Lukwangule Plateau.

The Uluguru Mountains are characterized by an oceanic rainfall pattern. The mountains receive short rains (*Vuli*) from October to December and the heavy long rains (*Masika*) from March to May. Estimated rainfall on the eastern slopes of Uluguru South is 2500–4000 mm/year, whereas on the western slopes, rainfall is estimated at 2000 mm/year. Mist and clouds occur throughout the year and are important sources of dry season moisture in higher altitude forests (Pócs, 1976a). The mean annual temperature in the Uluguru South is about 24.3°C with small seasonal variation. At lower altitudes, mean temperature ranges from 21.1°C to 26.5°C, whereas frost occurs above 2100 m in the Uluguru Mountains (Pócs, 1976b).

The altitudinal distribution of African amphibian fauna is well studied in southern Africa. Some of the comprehensive broad-scale studies in the altitudinal distribution of amphibians in Africa include those by Poynton and Broadley (1991), Poynton and Boycott (1996), and Poynton (1992, 2003). In the

Uluguru Mountains, the earliest inventory was carried out by Barbour and Loveridge (1928). Subsequent studies were carried out by Doggart et al. (2004) followed by other collectors (mainly Frontier Tanzania). Despite these studies, there has been little effort to determine the altitudinal distribution of amphibians in the Uluguru Mountains. This study attempts to determine the altitudinal distribution of amphibians in the Uluguru South Mountains. The core data used in this study come from an altitudinal transect that was established on the western slopes of this range. The paper also reviews what is known of the Uluguru South Mountains.

Materials and Methods

Amphibians were studied along an altitudinal gradient on the western slopes of the Uluguru South Mountains from 1000 m to the Lukwangule Plateau at about 2634 m. The surveys were conducted between 2001 and 2003. Five altitudinal zones were chosen and surveyed intensively, including 1000, 1200, 1500, 2000, and 2500 m (Figure 1). The lowest forested site is found at 1200 m in the Shikurufumi Forest Reserve (Fig. 1). Shikurufumi Forest Reserve is a forest fragment at the foothill of the western slopes of the Uluguru South Mountains.

At 1000 m, surveys were conducted in September 2001 (dry season); and at 1200 m the surveys were conducted in March 2002 (wet season) and in August 2002 (dry season). At 1500 m, the surveys were conducted both in cultivated and forested areas. In the cultivated areas, surveys were done in September 2001; in forest, they were conducted in March 2002 and August 2002. At 2000 m, the surveys were conducted in September 2001 and March 2002, and at 2500 m, the surveys were conducted between March and April 2003 (wet season) and between June and July 2003 during the dry season. Details and locations of each site are given in Table 1.

Standard methods for surveying amphibians were used, including drift fences with pitfall buckets, plots, and audio-visual encounter surveys (Heyer et al., 1994). Six drift fences with pitfall buckets were set at each altitudinal zone for seven days. Each pitfall line consisted of 11 pitfall buckets set at 5-m intervals, and a drift fence of polythene bisected all of the buckets in the line (see Stanley et al., this volume). Pitfall lines were set to include different habitat types (i.e., cultivated areas, forests, forest edges, and grasslands). Buckets were checked at least once every day.

Pitfall lines cannot adequately sample all amphibians; they were supplemented with plot method and audio-visual encounter surveys. Ten plots of 5 by 5 m were established at each altitudinal zone. Plots were systematically set at each zone, and the interval between one plot and another was 50 m. Each plot was searched thoroughly for amphibians once every sampling season by four observers. Sampling involved searching for amphibians in leaf litter, between or within grass tussocks, on plant trunk and leaves, and by turning logs and stones. Digging underground (5–10 cm deep) was also done to ensure a thorough search. Audio-visual encounter surveys were conducted both during the day and night to detect amphibians not sampled by pitfall lines and plots. Amphibians found were identified and released after taking some voucher specimens. Material collected has been deposited in the Department of Zoology and Wildlife Conservation, University of Dar es Salaam, Tanzania; Natural History Museum, London; and Museo Tridentino di Scienze Naturali, Trento, Italy. Species were classified following the taxonomy of Frost et al. (2006).

Data Analysis

Composition of amphibian species in different altitudinal zones was compared using the Jaccard Similarity Index (S_J) (Ludwig & Reynolds, 1988). This index uses presence/absence data and is widely used to assess similarity of communities. S_J is frequently multiplied by 100%, and may be represented in terms of dissimilarity (i.e., D_J = 1.0 & minus; S_J). The similarity index values range from 0 (no species common to both communities) to 1.0 (all species found in both communities). A higher similarity index suggests greater similarity of species among communities.

It is represented by the formula

$$S_J = \frac{a}{(a+b+c+n)},$$

where S_J is the Jaccard similarity coefficient, a is the number of species common to (shared by) communities, b is the number of species unique to the first community, c is the number of species unique to the second community, and n is the number of species unique to community n.

Results

The study recorded a total of 21 amphibian species belonging to eight families on the western slopes of Uluguru South Mountains. Observations revealed differences in species composition at different altitudes. Certain species occurred at more than one altitudinal zone, whereas for some species, there was an altitudinal overlap.

Seven species were recorded at 1000 m, 12 species at 1200 m, 11 species at 1500 m, seven species at 2000 m, and five species at 2500 m. The pattern shows a general decrease in the number of species with increased altitude (Table 2). An exception is at 1000 m, which had fewer species than did 1500 m. Only one species (*Arthroleptis affinis*) was found to occur on all altitudinal zones on the western slopes of the Uluguru South Mountains from 1200 m and above. The submontane forest portion (800–1500 m) supported more amphibian species than montane or upper montane forest portions (Table 2).

The amphibian species compositions were clearly separated by altitude. The study sites that were adjacent to each other showed greater similarity in amphibian species composition than did sites distant from each other. Pairwise comparison of species composition between different altitudinal zones is as shown in Table 3.

Species Accounts

Family Arthroleptidae
Arthroleptis spp.

This is one of the most taxonomically difficult genera in East Africa due to its variable coloration and morphology. Its

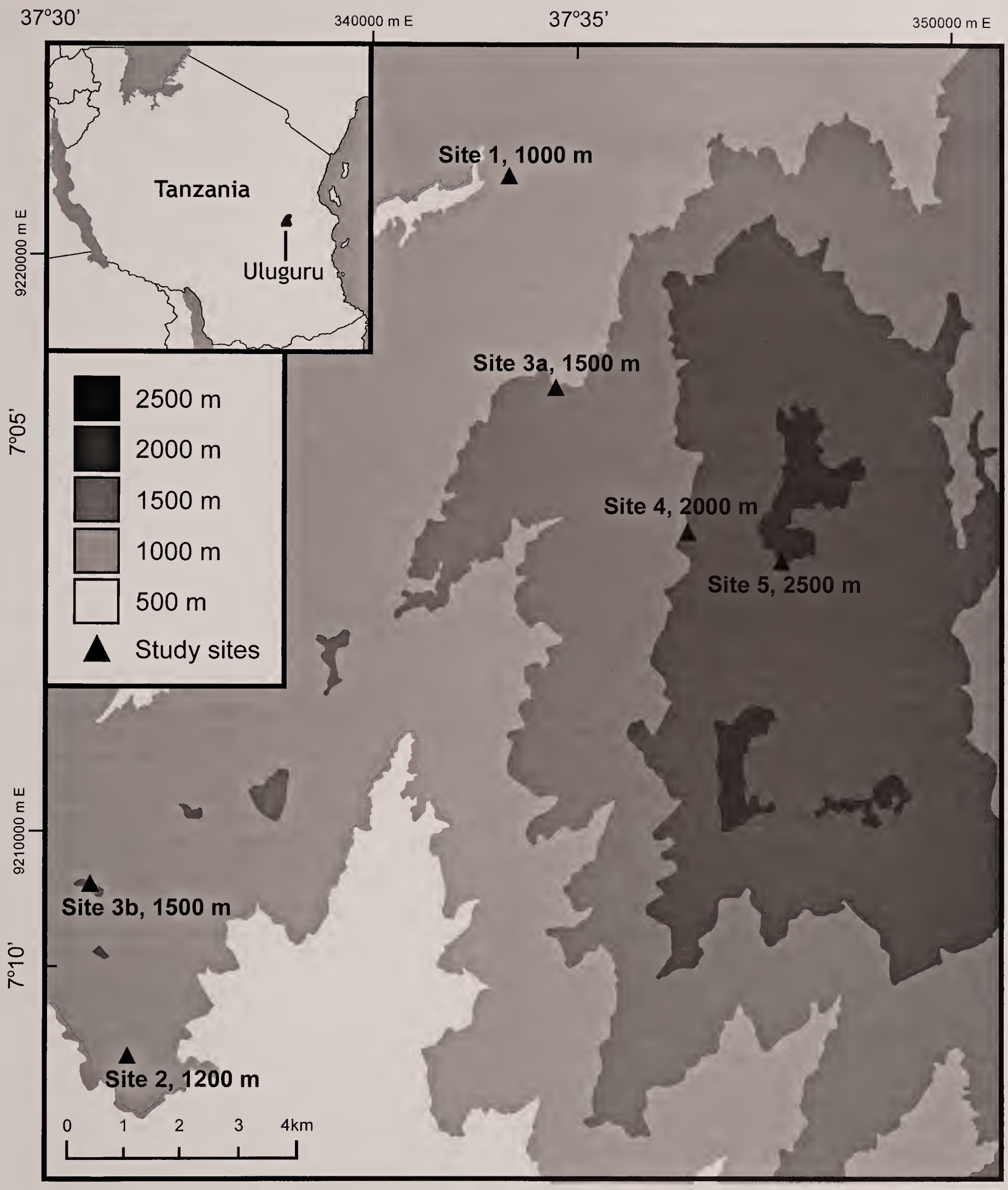

FIG. 1. Map of the western slopes of Uluguru South Mountains showing the study sites and elevations (Source: Tanzania Maps [Mgeta], Toposheet 201/1, Y742 Series, 1982).

taxonomy is not yet clearly settled. Breeding in known *Arthroleptis* species does not depend on water (Channing & Howell, 2006); members lay their eggs in nests under leaf litter and have no free-living tadpole stage.

***Arthroleptis affinis* Ahl, 1939**

This species is widely distributed along the altitudinal gradient in the Uluguru South Mountains. It has a very

TABLE 1. Location of the study sites on the western slopes of the Uluguru South Mountains, Tanzania.

Sampling site	Altitude (masl)[1]	Coordinates	Sampling time	Habitat type
1	1000	7°3.844′S, 37°34.254′E	1–10 September 2001	Cultivated land
2	1200	7°10.925′S, 37°30.744′E	1–10 March 2002 12–22 August 2002	Cultivated land and forest edge
3a	1500	7°5.155′S, 37°35.124′E	12–21 September 2001	Cultivated land
3b	1500	7°9.125′S, 37°30.565′E	1–20 March 2002 12–22 August 2002	Forest
4	2000	7°6.350′S, 37°36.700′E	23 September–2 October 2001 24 March–2 April 2002	Montane forest
5	2500	7°6.782′S, 37°36.850′E	11 March–9 April 2003 24 June–17 July 2003	Forest and grassland

[1] masl, meters above sea level.

wide altitudinal range and occupies habitats from the forest and cultivated areas and from the lowest sites, at 1200 m, to the upper montane forests at 2500 m. This species is terrestrial, found mostly under or on leaf litter in the forest. In other Eastern Arc Mountains it is known to occur from 190 to 2104 m (Poynton & Loader, 2008).

***Arthroleptis stenodactylus* Pfeffer, 1893**

Individuals of this species were found at 1000, 1200, and 1500 m (Table 4). This species inhabits the forest interior, forest edge, and cultivated areas. In forest, this species dwells mostly under leaf litter; large numbers of individuals were caught in pitfall buckets.

TABLE 2. Altitudinal distribution of amphibian species on the western slopes of the Uluguru South Mountains. X means species detected; blank means undetected.

	Altitude (m)				
Family/Species	**1000**	**1200**	**1500**	**2000**	**2500**
Arthroleptidae					
Arthroleptis affinis		X	X	X	X
Arthroleptis stenodactylus	X	X	X		
Arthroleptis xenodactyloides	X	X	X		
Leptopelis parkeri				X	
Brevicipitidae					
Breviceps mossambicus		X			
Callulina kreffti		X	X		
Probreviceps loveridgei		X	X		
Probreviceps uluguruensis				X	X
Spelaeophryne metlineri		X			
Bufonidae					
Amietophrynus gutturalis	X	X	X		
Nectophrynoides viviparus				X	X
Nectophrynoides laevis				X	
Nectophrynoides sp.					X
Hyperoliidae					
Hyperolius puncticulatus	X	X	X		
Kassina senegalensis		X			
Phrynobatrachidae					
Phrynobatrachus natalensis	X	X	X		
Phrynobatrachus udzungwensis			X		
Ptychadenidae					
Ptychadena oxyrhynchus	X				
Strongylopus fuelleborni					X
Pyxicephalidae					
Amietia angolensis	X	X	X	X	
Caeciliidae					
Scolecomorphus uluguruensis			X	X	
No. of species	**7**	**12**	**11**	**7**	**5**

TABLE 3. Comparison of amphibian community similarity in different altitudinal zones (m) on the western slopes of Uluguru South Mountains using Jaccard's Index (S_J).

	1000	1200	1500	2000	2500
1000	1	0.75 (75%)	0.67 (67%)	0	0
1200		1	0.64 (64%)	0.14 (14%)	0.06 (6%)
1500			1	0.20 (20%)	0.07 (7%)
2000				1	0.33 (33%)
2500					1

***Arthroleptis xenodactyloides* Hewitt, 1933**

Individuals of this species were found at 1000, 1200, and 1500 m (Table 4). It is a terrestrial species that inhabits both the leaf litter in the forest and cultivated areas.

***Leptopelis parkeri* Barbour & Loveridge, 1928**

Leptopelis parkeri is a tree frog that inhabits the forest at an altitude of 2000 m. It was found within the leaf axils of wild bananas filled with water. Eggs, recovered with the adult frogs from the leaf axils of wild bananas, could be the eggs of *Leptopelis*. The eggs were small and pigmented; however, it is difficult to state with certainty that they were *L. parkeri* eggs without further investigation. This species exhibits sexual dimorphism. Males are grayish to brownish or olive green with a conspicuous yellow pattern forming irregular transverse bands; females possess a uniform olive-green dorsum.

Brevicipitidae

***Breviceps mossambicus* Peters, 1854**

Individuals of this species were found in the cultivated areas at 1200 m, especially during the dry season, and were mainly found in the leaf litter.

***Callulina kreffti* Nieden, 1911**

This species was recorded at 1200 and 1500 m. It was found both in forest and farmland habitats at 1500 m, and at 1200 m only in the forest edge. Individuals were found in rotten logs and leaf axils of wild and cultivated banana plants. Many individuals were either opportunistically collected or visually encountered; none were collected in pitfalls.

***Probreviceps loveridgei* Parker, 1931**

Individuals of this species were found at 1200 and 1500 m in the Shikurufumi Forest Reserve. It inhabits both forested and cultivated areas at 1500 m, but only in the forest edge at 1200 m. Like many other leaf-litter frogs, breeding does not take place in the water. The females lay their eggs under leaf litter, and the young develop directly into adults (Müller et al., 2007). Eggs were recovered from the leaf litter throughout the study, indicating that this species breeds through the year.

***Probreviceps uluguruensis* (Loveridge, 1925)**

This species was collected from 2000 m to the Lukwangule Plateau. It is endemic to the Uluguru Mountains and is found in leaf litter, underground chambers in the forest, and below grass tussocks on the Lukwangule Plateau. Morphologically, *Probreviceps uluguruensis* is highly variable in color and pattern.

***Spelaeophryne methneri* Ahl, 1924**

Only a single adult female measuring 31 mm snout–vent length was collected over the entire sampling period in cultivated land at 1200 m.

Family Bufonidae

***Amietophrynus gutturalis* (Power, 1927)**

Individuals of this species were found at lower altitudes at 1500 m and below (Table 4). This species is highly versatile; it can inhabit various habitat types from degraded forests, moist savanna, and agricultural areas to human settlements. In the study area, this species was restricted to the cultivated land. No *A. gutturalis* were recorded in the forest habitat throughout the study period. Males were found calling at night from wetter areas and ephemeral water pools in the cultivated land at 1000, 1200, and 1500 m. The calls intensified during the wet season, especially after rain.

***Nectophrynoides laevis* Menegon *et al.*, 2004**

This species is restricted to the upper elevations at 2000 m. *Nectophrynoides laevis* appears to have a restricted distribution in the Uluguru South Mountain forest and is only known from one specimen. Nothing is known about its breeding biology and breeding behavior (Menegon et al., 2004). It is a tree frog that inhabits the forest habitat and the type was found on vegetation about 1 m off the ground.

***Nectophrynoides viviparus* Tornier, 1905**

In the Uluguru South, this species is restricted to the upper montane forest from 1900 m to the Lukwangule Plateau. Individuals were found under or on leaf litter and in grass tussocks on the plateau. They were also observed climbing and calling on vegetation to about 1 m off the ground. This species is highly variable in color pattern and morphology. Advertisement calls produced by frogs at 2000 and 2500 m differed dramatically. The advertisement call of the male recorded at 2000 m was low-pitched and composed of a sequence of 23 discrete notes. Mean call duration was 54 ms (range, 43–87, n = 3). The fundamental and dominant frequencies were dissimilar for each note at 1.698 and 1.727 kHz, respectively. *Nectophrynoides viviparus* from the Lukwangule Plateau (2500 m) has a characteristic call of high-pitched clicks, "cluck" "cluck," composed by a series of six to eight notes. Mean call duration was 475 ms (range, 128–833, n = 6) with fundamental and dominant frequencies of 2.386 and 2.427 kHz, respectively. The differences in calls suggest that the two forms may be distinct; this requires further investigation.

***Nectophrynoides* sp.**

During the study, three specimens were collected in a forest patch on the Lukwangule Plateau. These individuals were distinct from other known taxa and may tentatively be considered new species. These were found in a hole in a standing dead tree.

TABLE 4. Number of individuals of different amphibian species found during the surveys in different altitudinal zones (m) on the Uluguru South Mountains. Blank cells indicate no individuals of the species were detected.

	1000		1200		1500		2000		2500	
Family/Species	**Dry**	**Wet**	**Dry**	**Wet**	**Dry**	**Wet**	**Dry**	**Wet**	**Dry**	**Wet**
Arthroleptidae										
Arthroleptis affinis				6		5	2	15		3
Arthroleptis stenodactylus	1		31	36	4	11				
Arthroleptis xenodactyloides	12		6	17	6	12				
Leptopelis parkeri							25	7		
Brevicipitidae										
Breviceps mossambicus			9	5						
Callulina kreffti				1	5					
Probreviceps loveridgei			5	40	6	9				
Probreviceps uluguruensis							16	63	45	26
Spelaeophryne metlneri				1						
Bufonidae										
Amietophrynus gutturalis	9		21	1	5	7				
Nectophrynoides viviparus							7	59	39	31
Nectophrynoides laevis								1		
Nectophrynoides sp.										3
Hyperoliidae										
Hyperolius puncticulatus	5		14	22	4	27				
Kassina senegalensis				1						
Phrynobatrachidae										
Phrynobatrachus natalensis	7		1	10	1	27				
Phrynobatrachus udzungwensis						12				
Ptychadenidae										
Ptychadena oxyrhynchus	1									
Strongylopus fuelleborni									27	128
Pyxicephalidae										
Amietia angolensis	8		2	8	4	1	8	10		
Caeciliidae										
Scolecomorphus uluguruensis				3		1				

Family Hyperoliidae
***Hyperolius puncticulatus* (Pfeffer, 1893)**

This tree frog was recorded in cultivated areas at 1000 and 1200 m and at the forest edge at 1500 m but was not found in the forest interior. It is highly variable in color and pattern (Harper et al., 2010). Males were calling on vegetation about 0.5–1 m high above the ground near streams.

***Kassina senegalensis* (Duméril and Bibron, 1841)**

This species was collected in pitfall buckets at forest edge at 1200 m during the wet season.

Family Phrynobatrachidae
***Phrynobatrachus natalensis* (Smith, 1849)**

This species was found at 1000, 1200, and 1500 m near stream banks in cultivated lands and at forest edge at 1500 m.

***Phrynobatrachus uzungwensis* Grandison & Howell, 1983**

This species was only found in forest habitat during the wet season at 1500 m, specifically in the forest floor leaf litter. Breeding probably occurs in the rainy season. During this period many individuals were collected from the forest floor; none were collected in dry season.

Family Ptychadenidae
***Ptychadena oxyrhynchus* (Smith, 1849)**

This species was collected in the degraded areas (cultivated areas) at 1000 m. It was found in abandoned farms dominated by grasses during the dry season.

Family Pyxicephalidae
***Amietia angolensis* (Bocage, 1866)**

This is a common, semi-aquatic species that occupied cultivated areas at 1000, 1200, and 1500 m to the forested habitat at 2000 m. It is highly associated with water, being found in rivers and along streams.

***Strongylopus fuelleborni* Nieden, 1911**

This species is restricted to the Lukwangule Plateau grasslands in the Uluguru South Mountains (~2400–2500 m). Most individuals were observed near water and only a few were found away from a water source. Males call from the grassland swamps and have a characteristic call of a high-

pitched "pip" uttered once or in a short burst of three or four. This species was removed from synonymy with *Rana merumontana* Lönnberg, 1910, by Poynton (2004).

Family Caeciliidae
***Scolecomorphus uluguruensis* Barbour & Loveridge, 1928**

This caecilian was only found in forests from 1500 to 2000 m. Individuals were mostly captured in pitfall buckets and also found in plots during the wet season.

Discussion

A total of 21 species were recorded during this study. Four additional species of amphibians are known to occur in the Uluguru South Mountains but were not recorded during the study. These include: *Nectophrynoides cryptus* (Howell, 1993), *N. pseudotornieri* (at 2040 m; Menegon et al., 2004; Frontier Tanzania, 2005), *Hoplophryne uluguruensis* (at 2040 m; Frontier Tanzania, 2005), and *Petropedetes yakusini* (900–1820 m; Frontier Tanzania, 2005). The unrecorded species are perhaps rare or highly cryptic and therefore were not detected. Of the 25 amphibian species known from Uluguru South, five species, including *N. cryptus, N. laevis*, *N. pseudotornieri*, *Probreviceps uluguruensis,* and *Scolecomorphus uluguruensis,* are endemic to the Uluguru Mountains. The other five species found in the Uluguru, including *Callulina kreffti*, *N. viviparus*, *P. loveridgei*, *P. yakusini,* and *Leptopelis parkeri,* are endemic to the Eastern Arc Mountains in general (see Poynton et al., 2006). The Eastern Arc Mountains are known for high endemism in many taxonomic groups (Dinesen et al., 2001), explained as the consequences of stable local conditions (Burgess et al., 2007). These stable conditions are the result of historical processes in the Eastern Arc Mountains that would result in species replacement patterns that are congruent across many evolutionary lineages (Burgess et al., 2007).

The data indicate a general decline in the number of amphibian species with increasing elevation. The decline in amphibian species richness and diversity with an increasing elevation in tropical mountain forests has been reported across the globe (e.g., Brown & Alcala, 1961; Fauth et al., 1989). The decrease in temperature, precipitation, and productivity are thought to be the most critical factors limiting species diversity at higher elevations (Rahbek, 1995), although how the environmental variables impinge on the life of amphibians is not fully understood (Loader et al., 2004).

Many of the species found below 1500 m are widely distributed throughout lowland areas in East Africa (e.g., *Arthroleptis stenodactylus, A. xenodactyloides, Amietophrynus gutturalis,* and *Ptychadena oxyrhynchus*; see Channing & Howell, 2006), whereas those found above 1500 m, including *N. laevis N. viviparus*, *L. parkeri,* and *P. uluguruensis,* have a more restricted distribution. This shows distinctiveness of highland amphibian fauna from those at the lowland. Recent taxonomic studies elsewhere in the Eastern Arc Mountains have shown distinctiveness in some of the isolated populations, such as *Callulina* (Loader et al., 2010). In the Uluguru South Mountains, at least three species of *Nectophrynoides* are known, one of which, *N. viviparus*, was found at more than one altitudinal zone (Table 2). The calls of males at 2000 m were different from those at 2500 m, suggesting that the two populations might be genetically distinct. Further investigation is needed to determine their status. The altitudinal limit for lowland and montane forest herpetofauna has been reported from other areas, including Kibale National Park (Vonesh, 2001), Mahenge Mountains (Loader et al., 2004), Udzungwa Mountains (Menegon & Salvidio, 2005), and across southern and eastern Africa (Poynton & Broadley, 1991; Poynton, 1992, 2003; Poynton & Boycott, 1996). According to Poynton et al. (2006), the differences between montane and lowland amphibian assemblages appear to be long standing, broadly characterized respectively by cool temperate relicts and widespread generalists rather than local elimination of species common to both.

The number of amphibian species at 1200 m was twice the number of species found at 1000 m. Sampling at 1000 m included cultivated areas in which all natural vegetation had been cleared and replaced by crops, whereas at 1200 m, sampling included both cultivated areas and forest edge. Most of the species found at 1200 m were forest-dependent species (Howell, 1993) that cannot tolerate disturbed habitats. Furthermore, the 1000-m zone was only sampled during the dry season, whereas the 1200-m zone was sampled during both dry and wet seasons. These reasons may explain the smaller number of species at 1000 than at 1200 m. The effect of habitat degradation on composition and diversity of species has been stated (Hillers et al., 2008). Cultivation in the Uluguru Mountains is normally associated with the removal of plant cover, affecting the thickness of leaf litter, humidity, and canopy cover. Species like *Probreviceps loveridgei*, *Spelaeophryne methneri,* and *Breviceps mossambicus* were found at 1200 m but not at 1000 m. These species are commonly associated with leaf litter (Channing & Howell, 2006); it seems human-induced clearance of fields at 1000 m may have eliminated them. Hillers et al. (2008) showed that opening the canopy changes the microclimate and most likely exceeds the physiological capability of several frog species, and this can lead to a reduction in diversity of amphibian species. This study demonstrates rather restricted habitat and altitudinal distribution of some montane endemics, which raises conservation concerns, especially as the increasing loss of habitat at lower altitudes and, continuing toward higher altitudes, will eventually eliminate some species.

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Chapter 7

Herpetofauna of Montane Areas of Tanzania. 3. Amphibian Diversity in the Northwestern Eastern Arc Mountains, with the Description of a New Species of *Arthroleptis* (Anura: Arthroleptidae)

Simon P. Loader[1], John C. Poynton[2], Lucinda P. Lawson[3], David C. Blackburn[4], and Michele Menegon[5,6]

[1]*Institute of Biogeography, University of Basel, Basel, Switzerland*
[2]*Department of Zoology, The Natural History Museum, London SW7 5BD, United Kingdom*
[3]*Department of Zoology, Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, IL 60605, USA*
[4]*Natural History Museum and Biodiversity Institute, University of Kansas, Lawrence, KS 66045, USA*
[5]*Tropical Biodiversity Section, Museo Tridentino di Scienze Naturali, Via Calepina 14, I–38100, Trento, Italy*
[6]*Department of Environmental & Geographical Sciences, Manchester Metropolitan University, Manchester, United Kingdom*

Abstract

Amphibians of the Eastern Arc Mountains are poorly known, apart from those of the East Usambara, Uluguru, and Udzungwa Mountains. Here, we detail specimens collected in the northwestern Eastern Arc Mountains (West Usambara, South Pare, and North Pare) over the past 100 years. Although not comprehensive, the list is compiled from specimens held at institutions in Europe and the United States and in personal collections; it includes most of the specimens known from this area. From these specimens, we describe one new species of the frog genus *Arthroleptis* and discuss other specimens that may represent new species. We add substantially to the known diversity in these areas. Using the compiled species list, we assess species diversity and relate the differences to sampling bias and possible biogeographic differences among the mountains. The future preservation of amphibians across this area is of concern given the increasing loss of forest.

Introduction

East African mountains are noted for their high levels of biodiversity (e.g., Burgess et al., 2007). In northern Tanzania, the East Usambara section of the Eastern Arc Mountain chain (EAM) has been a focus of collecting for a century (Howell, 2000) and shows a high degree of endemicity that has made it one of the main conservation priorities in the region. Northwest of the East Usambara, the EAM continues as three mountain ranges showing topographical complexity: the West Usambara, South Pare, and North Pare (Fig. 1). These have a similar geological origin to the East Usambara mountain complex (Griffiths, 1993) and contain evergreen rainforest assemblages (Howell, 1993; Lovett, 1993). These three blocks have received only patchy attention and are poorly understood biologically compared with the East Usambara (Burgess et al., 2007). This is particularly true of the amphibian fauna (Grandison, 1983), which has proved to be conspicuously rich in the EAM (Poynton et al., 2007; Andreone et al., 2008). The primary aim of this paper is to consolidate our knowledge of amphibian diversity in these three mountain regions and thus highlight this relatively poorly studied area.

The first notable herpetological collections from the EAM were made by early German explorers around the turn of the 20th Century (Howell, 2000). The focus, as today, was mainly in areas around the East Usambara (Grandison, 1983), principally in and around Amani, a German medical field station. The earliest herpetological collections made in the West Usambara were in Philipshof (=Magamba, near Lushoto, West Usambara, Tanzania), Mombo (Nieden, 1915) and Ambangulu (reported in Nieden, 1913; Bauer et al., 2006). But not until Barbour and Loveridge's (1928) pivotal paper on the fauna of the Uluguru and Usambara Mountains were the amphibians northwest of the East Usambara discussed explicitly. Loveridge collected most intensively in the East Usambara but also sampled areas in the West Usambara (Philipshof and Bumbuli). Loveridge recorded only two and eight species, respectively, from these localities (Barbour & Loveridge, 1928). After this period, there was a hiatus in herpetological collecting in this area.

From 1970 onward, short surveys have been made fairly frequently in the West Usambara Mountains (Grandison, 1983). Among specimens recorded in this paper are collections by A. G. C. Grandison, who surveyed Mazumbai in 1973; K. M. Howell collected in the 1980s and 1990s; R. C. Drewes and J. V. Vindum of the California Academy of Sciences surveyed Mazumbai Forest Reserve (FR), Baga II FR, and Lushoto FR in 1988; A. Schiøtz surveyed Mazumbai during the 1970s

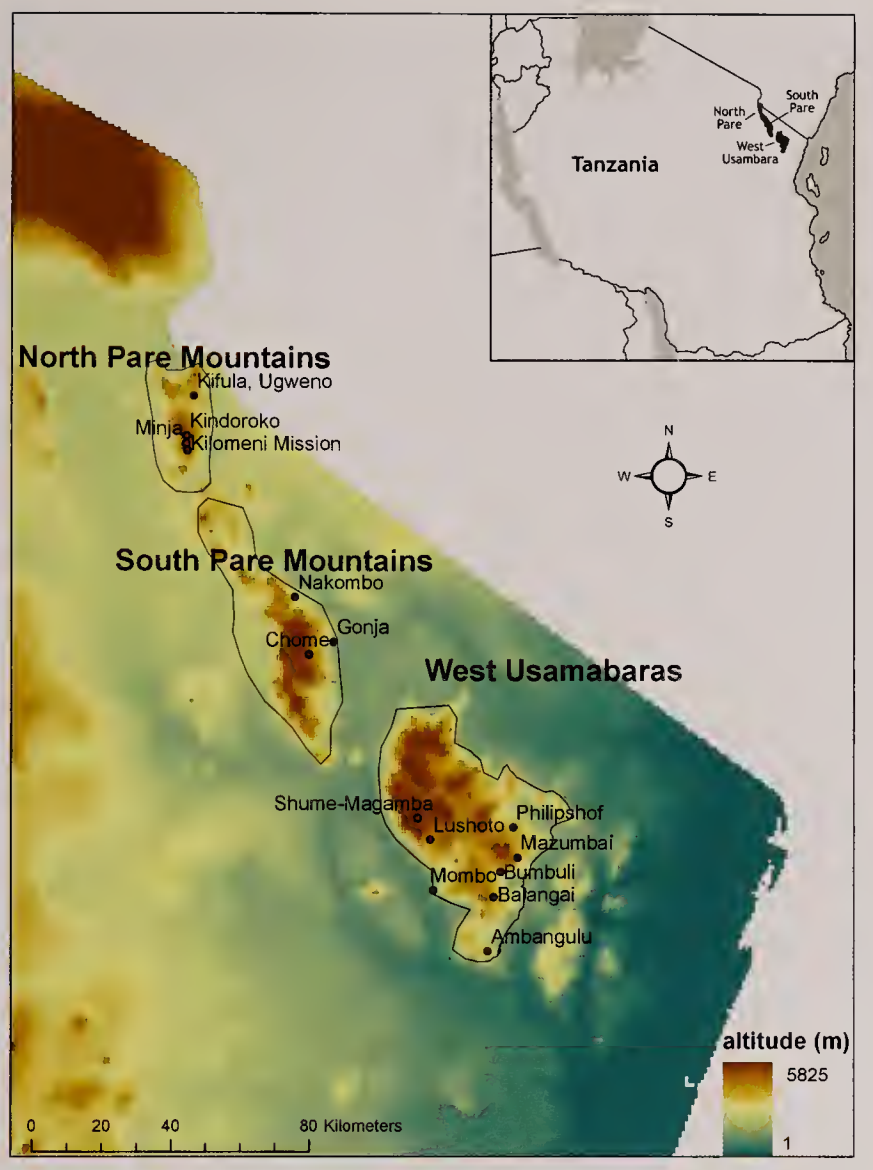

FIG. 1. Map of the northern Eastern Arc Mountains of Tanzania.

through 1990s; J. Rasmussen, M. Anderson, and M. Vestergaard surveyed Mazumbai in 1992; W. T. Stanley and S. M. Goodman from the Field Museum of Natural History (FMNH, Chicago, IL) surveyed Ambangulu at various times between 1991 and 1993; M. Coe collected specimens in the West Usambara; A. Channing and R. O. de Sá surveyed Mazumbai FR in 2000 and 2009; S. P. Loader and J. Mariaux surveyed Mazumbai in October 2001; S. P. Loader, J. Mariaux, and D. J. Gower surveyed Ambangulu in May 2002; and a combined FMNH and MCZ (Museum of Comparative Zoology, Cambridge, MA) expedition conducted by L. Lawson, L. Mahler, and B. Zimkus (2007) surveyed Mazumbai, Shume-Magamba, and Ambangulu. Other surveys may have been conducted but remain unknown to us.

The amphibians and reptiles of the Pare Mountains have received substantially less attention. K. M. Howell and C. A. Msuya made the first surveys in the North Pare in the 1970s and into the 1980s. N. Cordeiro made collections of amphibians in the North Pare in July 1993, and at the same time, W. T. Stanley and S. M. Goodman from FMNH and C. A. Msuya of the University of Dar es Salaam, Tanzania, surveyed the South Pare. A year later, W. T. Stanley made further collections at higher altitudes in the South Pare. An Mkomazi Ecological Research Programme collected two species in the South Pare outside the Mkomazi Reserve, Tanzania. Most recently S. P. Loader, J. Mariaux, and D. J. Gower of BMNH (Natural History Museum, London) and MHNG (Muséum d'histoire naturelle de Genève) and M. Menegon of Trento Museum (2007–2008) surveyed the North and South Pare.

From the surveys conducted in the West Usambara and Pares, the geographical distributions of a number of species have been extended (summarized in Howell, 1993; Burgess et al., 2007), and eight amphibian species have been described: *Arthroleptis lonnbergi* Nieden, 1915; *Hyperolius tanneri* Schiøtz, 1982; *Arthroleptis tanneri* Grandison, 1983; *Callulina kisiwamsitu* de Sá et al., 2004; *Arthroleptis fichika* Blackburn, 2009; *Callulina laphami* Loader et al., 2010; *Callulina stanleyi* Loader et al., 2010; and *Callulina shengena* Loader et al., 2010. In total, four species are endemic to the West Usambara, three species to the South Pare including our new *Arthroleptis*, and one species to the North Pare.

Given the number of surveys, it might be assumed that we have a relatively good understanding of the amphibians in this region, particularly the West Usambara. However, the recorded distribution of many taxa across the Eastern Arc is currently confused and certainly incomplete (Poynton et al., 2007); thus, records of even reputedly common species should be re-examined closely. By citing specimens and their locality data, we intend to establish a comprehensive list of amphibians of West Usambara and Pare Mountains. Additionally, we describe one new species and outline specimens putatively identified as being distinct and not assignable to any currently described taxon. All specimen identifications were made either by authors of the paper or communicated to us by colleagues (A. Channing and B. M. Zimkus). This list is therefore necessarily preliminary—detailed taxonomic assessment is still required in some taxa. Overall, we aim to establish a thorough summary of taxonomic information on the amphibians in this area, which we hope will encourage researchers to conduct further field surveys and detailed taxonomic work on specimens from these mountains.

Materials and Methods

Material was examined from the following institutions or personal collections: Alan Channing Field Series (AC); Natural History Museum, London (BMNH); California Academy of Sciences, San Francisco (CAS); Field Museum of Natural History, Chicago (FMNH); Lucinda Lawson Field Series (LL); Museum of Comparative Zoology, Harvard University (MCZ); Muséum d'Histoire Naturelle, Geneva (MHNG); Museo Tridentino di Scienze Naturali, Trento (MTSN); University of Michigan Museum of Zoology, Ann Arbor (UMMZ); United States National Museum, Washington, D.C. (USNM); Humboldt-Universität, Zoologisches Museum, Berlin (ZMB); Zoological Museum of Copenhagen (ZMUC). The taxonomy largely follows that of Frost (2010), with the exception of several new species that were described recently (Loader et al., 2010). Some *Arthroleptis* specimens could not be identified, either because of poor state of preservation or because they are juveniles. The specimens we were unable to identify include: CAS 169383–93, Baga II FR; CAS 173798, Mazumbai FR; CAS 200511–12, Mazumbai FR. A gazetteer lists all localities given for each specimen (degrees, minutes, seconds); elevation (m) is provided when known. Certain localities visited on multiple occasions are numbered to differentiate between each one (e.g., Ambangulu FR, Mazumbai FR, and Chome FR). Further specific details of these localities are given in the gazetteer section.

List of the Amphibians of the West Usambara and South and North Pare Mountains

Order Anura
Family Arthroleptidae
***Arthroleptis* spp.**

Arthroleptis is one of only three genera of widespread African frogs for which comprehensive taxonomic and geographic sampling has been attempted for a molecular phylogenetic analysis (Blackburn, 2008), the others being *Xenopus* and *Plurynobatrachus* (Evans et al., 2004; Zimkus et al., 2010). Blackburn (2008, 2009a) revealed that *Arthroleptis* species from the EAM and elsewhere in East Africa represent at least two radiations. Taking morphological characters also into account, one radiation comprises miniature species (snout–vent length < 25 mm) with small inner metatarsal tubercles not (or barely) longer than the length of the subarticular tubercles; EAM species include *A. xenodactylus, A. xenodactyloides, A. fichika*, and *A. kidogo*. Another radiation comprises medium- to large-sized species with inner metatarsal tubercles at least twice as large as the subarticular tubercles (but not longer than the first toe); representatives in the EAM are *A. affinis, A. reichei*, and *A. nguruensis*. Another species in this region with an inner metatarsal tubercle longer than the first toe is represented by *A. stenodactylus*. We describe here a species that exhibits morphology intermediate between that of the two recognized clades, thus making its relationship obscure. This new species is even more exceptional in lacking an externally visible tympanum; instead, the otic region is fully occupied by jaw musculature.

***Arthroleptis anotis* sp. nov.**
Figure 2a–d, dorsal, and lateral views

Holotype—BMNH 2000.732 (field number KMH 19583), a gravid female collected 19 November 1999 by K. M. Howell in the Chome Forest Reserve, South Pare Mountains, Tanzania, ca. 1900 m elevation, 4°18′S, 37°53′E (see Fig. 2a,d).

Paratype—BMNH 2000.731 (field number KMH 19581), a female with developing ova collected 19 November 1999 by K. M. Howell in the Chome Forest Reserve, South Pare Mountains, Tanzania, ca. 1900 m elevation, 4°18′S, 37°53′E.

Diagnosis—A miniature *Arthroleptis* (snout–vent length < 25 mm) that is distinguished from all other *Arthroleptis* (sensu Blackburn, 2008) by lacking an externally visible tympanum (see Fig. 2b,c). In other respects, the species presents typical *Arthroleptis* features (e.g., Frétey, 2008; Zimkus & Blackburn, 2008) by having a dorsal skin ridge (or "raphe"), a dorsal "hourglass pattern," and large unpigmented eggs; lacking interdigital pedal webbing; and having only one metatarsal tubercle (i.e., inner metatarsal tubercle).

Measurements of Holotype (and Paratype)—Measurements taken by one researcher (J.C.P) using mechanical calipers accurate to 0.1 mm. Snout–urostyle length (SUL) 22.9 mm (20.2 mm), snout–vent length 23.6 mm (21.2 mm), head width 18.8 mm (17.9 mm), internarial distance 2.8 mm (2.4 mm), tibia length 10.5 mm (9.4 mm), foot length 10.2 mm (9.4 mm), length of inner metatarsal tubercle 1.0 mm (1.0 mm), oval in shape, not ridged, length of other pedal subarticular tubercles less than 0.9 mm, inner toe length 1.6 mm (1.2 mm), length of fourth toe 5.7 mm (5.6 mm), length of third finger 3.0 mm (2.9 mm). Tips of fingers and toes slightly expanded with rounded discs, toe discs with circum-marginal grooves; disc width on toe four 0.6 mm, width of distal tubercle of toe four 0.4 mm, disc width on finger three 0.5 mm, width of distal tubercle of finger three 0.4 mm (toes and fingers desiccated, compromising accuracy of measurement). Diameter of eggs 2.1 mm.

Description of Holotype—No externally visible tympanum; tympanic area occupied by extensive adductor musculature with no tympanic membrane or columella evident. Reflected skin shows no tympanic impression. Tongue heart-shaped, no median papilla, no vomerine teeth, premaxillary and maxillary teeth present. Inner metatarsal tubercle ovoid and not projecting as a flange. Interocular area to rostral tip light-colored with some darker flecks. Dorsal skin ridge marked by a light line. Markings include a pair of light, diverging post-scapular patches, a pair of dark patches beside the ilia, and a dark transverse bar on each crus. Dark band extending behind eye to above the region that would normally be occupied by tympanum to level of jaw articulation. In ventral view, gular region immaculate, pectoral region with dark brown spots, most of abdomen darkened by a single large brown patch.

Variation—The paratype agrees morphologically with the holotype. The snout is lighter in color, but with more flecks present than in the holotype (see Fig. 2e,f). As in the holotype, the paratype exhibits the dorsal hourglass pattern typical of many *Arthroleptis*, but with a larger light area in the scapular region that extends on to the sides. A dark patch extends along either side of the ilia. The gular, pectoral, and abdominal regions are almost immaculate in the paratype.

Coloration in Life—No description of the color in life of the holotype was provided. The paratype was described as being brown with a relatively darker brown hourglass pattern on the dorsum and a red-orange venter.

Natural History—The only two specimens were collected from the leaf litter in montane forest in Chome Forest Reserve through casual visual surveys. There is no information regarding any other aspects of its biology (e.g., calls, behavior).

Conservation Status—*Arthroleptis anotis* is currently known only from Chome Forest at ca. 1900 m. If its distribution is restricted to the South Pare Mountains (maximum estimated forest cover between 139 to 333 km^2; Table 2), then it should be considered of high conservation concern.

Etymology—The specific epithet derives from Greek (*an-*, without; *otos*, ear) and relates to the fact that this is the only species of *Arthroleptis* known to lack an externally visible ear.

***Arthroleptis affinis* Ahl, 1939**

Records—**WEST USAMBARA**, MCZ A-13167 (Philipshof).

Remarks: Until very recently, all medium- to large-sized *Arthroleptis* in the MCZ collections from the EAM were identified as *Arthroleptis adolfifriederici*, a species with a complicated taxonomic history (Blackburn et al., 2009). These misidentifications contributed to erroneous distribution maps for *A. adolfifriederici* in a recent review of East African amphibians (Channing & Howell, 2006; K. Howell, pers. comm.); these specimens even included one designated as a paratype of *A. tanneri* by Grandison (1983). Poynton and Loader (2008) did not record specimens of *A. affinis* from the West Usambara or Pare Mountains but pointed out the many taxonomic difficulties with large-bodied *Arthroleptis* in the

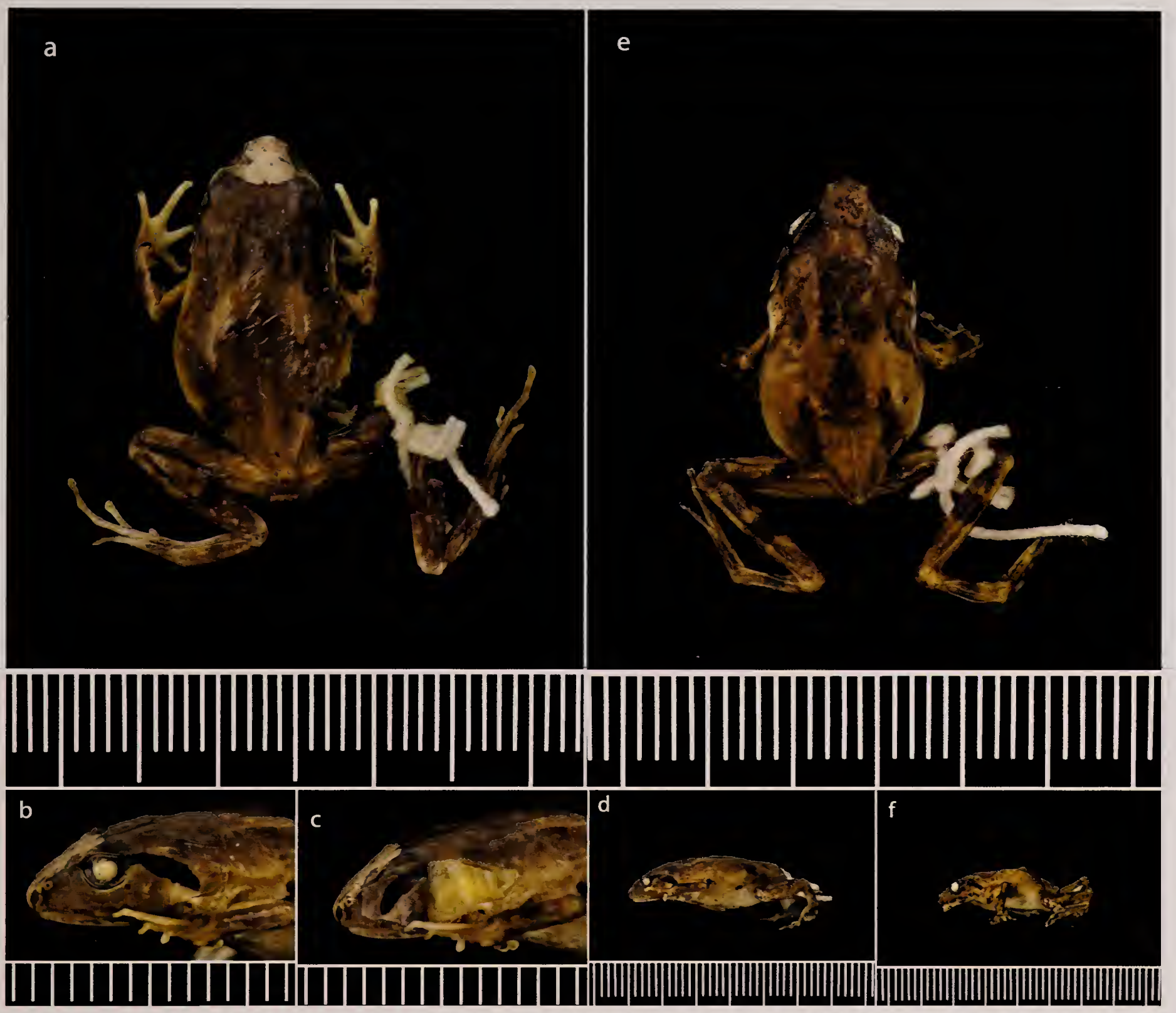

FIG. 2. Photographs of *Arthroleptis anotis* n. sp. in dorsal, and lateral view of head: (**a–d**) Holotype (BMNH 2000.732): (**e, f**) paratype (BMNH 2000.731). Scale bar = 1 mm.

EAM. The single male specimen (MCZ A-13167; 27.8 mm snout–vent length) recorded here from the West Usambara, which was collected alongside a paratype of *A. tanneri* (Barbour & Loveridge, 1928), is, to our knowledge, the only specimen from these mountains that is morphologically similar to *A. affinis*, the type locality of which is in the East Usambara.

***Arthroleptis fichika* Blackburn, 2009**

RECORDS—**WEST USAMBARA**, MCZ A-138384 (Mazumbai FR I); AC 2209, AC 2211 (Mazumbai FR II); BMNH 1974.225–28 (Mazumbai FR II); CAS 168829 (paratype; Baga II FR); **SOUTH PARE**, FMNH 251864 (Chome FR V); **NORTH PARE**: BMNH 2005.950 (Kindoroko FR).

REMARKS: This species was recently described by Blackburn (2009a), who noted that a single specimen (FMNH 251864) from the South Pare was highly genetically divergent (16.7%) from West Usambara populations of *A. fichika* with which it formed a clade in phylogenetic analysis. This single specimen was tentatively included in *A. fichika*, though it likely represents another cryptic species of miniature *Arthroleptis*. We add new specimen records of *A. fichika* from the type locality from Grandison's Mazumbai collection (BMNH 1974.225–228) and Channing's collection (AC 2209, 2211). Because several of these new records are males and the description of *A. fichika* was based only on females, we provide data on male traits. Of Grandison's four specimens, one is a male, BMNH 1974.227, snout–urostyle length 12.5 mm. The third finger is 2.0 mm long (16.4% SUL). The SUL of the females ranges from 15.1 to 14.3 mm; the length of the third finger ranges from 2.1 to 1.9 mm (average 13.5% SUL). The third finger of the male has several spines on the medial and dorsal surfaces; the second finger has fewer spines. One specimen (AC 2211; 13.9 mm snout–vent length) has small spines typical of *Arthroleptis* on the medial surface of the third finger (three on the right and approximately two on the left), but there is no evidence of spines in the inguinal region as

in many other *Arthroleptis* (Blackburn, 2009b). There is no obvious dimorphism in third finger length when comparing AC 2211 (12.9% of snout–vent length) to the female type specimens (11.1% and 13.3%). Furthermore, one specimen collected in the North Pare Mountains is tentatively included under this species. With just a single specimen and lack of DNA sequence data, the taxonomic evaluation of this population is preliminary, especially given the genetic differences between populations from the type locality and those from populations on other mountains (Blackburn, 2009a).

***Arthroleptis lonnbergi* Nieden, 1915**

Records—**WEST USAMBARA**, ZMB 24535 (holotype; Mombo).

Remarks: Recently, Pickersgill (2007) used call data to justify the resurrection of *A. lonnbergi* based on specimens from the East Usambara (Kambai and Longuza Forest Reserves) that are reportedly morphologically similar to *A. stenodactylus*. Unfortunately, these specimens are not (to our knowledge) deposited in a collection that is available for study. Thus, it is unclear whether specimens considered *A. stenodactylus* here correspond to *A. lonnbergi* (sensu Pickersgill, 2007). In addition, this resurrection was done without reference to the type and only specimen of *A. lonnbergi* (ZMB 24535) but rather because it was "the earliest applicable name [Pickersgill] could find." It should be noted that *A. lonnbergi* was erected by Nieden (1915) for a single specimen that he noted was morphologically similar to *A. stenodactylus* in all features except that it lacked a median tongue papilla. This is incorrect as examination of the holotype (probably an immature female; 29.6 mm snout–vent length) reveals a prominent median papilla at approximately a fourth of the distance to the posterior margin of the tongue. The specimen also has a prominent inner metatarsal tubercle, although it is not longer than the first toe as in most specimens of *A. stenodactylus*. We include this specimen in our account because the type locality is given by Nieden (1915) as "Mombo in Usambara," which is a town (ca. 440–460 m elevation) located at the base of the West Usambara. However, it is not impossible that the holotype of *A. lonnbergi* was collected in the mountains. Rather than redesignating *A. lonnbergi* as a junior synonym of *A. stenodactylus*, we take the position that further study employing detailed and statistical morphological analyses are needed to address possible cryptic diversity within *A. stenodactylus* and its past or present junior synonyms.

***Arthroleptis stenodactylus* Pfeffer, 1893**

Records—**WEST USAMBARA**, FMNH 248019 (Ambangulu FR III); MCZ A-13139 (Bumbuli), A-138370–79, A-138381 (Mazumbai FR I); **SOUTH PARE**, FMNH 251441–42 (Gonja FR), 251881, 255891 (Chome FR V).

Remarks: *Arthroleptis stenodactylus* is a widespread East African species occurring in forests, savanna woodlands, and even near urban areas, such as the campus of the University of Dar es Salaam (K. M. Howell, pers. comm.). This species has several junior synonyms, but until recently, there has been little investigation of patterns of diversity among populations referred to *A. stenodactylus* based on morphological evidence. Blackburn (2008) found that although *A. stenodactylus* was monophyletic, it contained one of the highest levels of intraspecific genetic divergence of the *Artlıroleptis* species surveyed in that study.

***Arthroleptis tanneri* Grandison, 1983**

Records—**WEST USAMBARA**, BMNH 1974.59 (holotype; Mazumbai FR II), 1974.50–63, 1974.200, 1982.525–36, R 7797–98 (paratypes; Mazumbai FR II), 1982.537–540 (paratypes; Shume-Magamba FR I), 1982.541 (paratype; Balangai FR), 2005.1336-42 (Mazumbai FR I); CAS 168820–21, 168825–27 (Baga II FR), 168823–24 (Mazumbai FR II); MCZ A-13166 (paratype; Philipshof); ZMUC R7731–68, R361395, R77837, R771060 (Mazumbai FR II).

Remarks: In contrast to what Channing and Howell (2006) reported, we know of no record of this species outside the West Usambara (Poynton & Loader, 2008). There is a radiation of medium- to large-sized *Arthroleptis* across the EAM (Blackburn, 2008; Poynton et al., 2008), and distinguishing species can be difficult (Poynton & Loader, 2008). Poynton and Loader (2008) show that the *A. tanneri* type was distinguishable from other species on the basis of head/tibia ratio, and Blackburn (2008) demonstrated that *A. tanneri* was genetically divergent from *A. affinis*, *A. nikeae*, and *A. reichei*, possibly not even forming a clade with these other EAM species.

***Arthroleptis xenodactyloides* Hewitt, 1933**

Records—**WEST USAMBARA**, CAS 168829 (Baga II FR), 200513–515 (Mazumbai FR II); FMNH 250446–51 (Ambangulu FR VII); **SOUTH PARE**, BMNH 2005.987–89 (Nakombo River), 2005.990–93 (Pare Forest), 2000.733 (Chome FR I); FMNH 251406–09, 251418 (lot of seven specimens), 251419–20 (lot of 12 specimens), 251421 (lot of 14 specimens), 251422–35 (Chome FR IV), 251443–44 (Gonja FR), 251863–68 (Chome FR V); MTSN 7545–46 (Chome FR II).

Remarks: *Arthroleptis xenodactyloides* is the most widespread species of miniature *Arthroleptis* in East Africa and has one of the largest elevational ranges of any East African frog (Poynton et al., 2007). A recent phylogeographic study has highlighted that populations of *A. xenodactylodes* from the northernmost EAM, including the Usambara Mountains, form a clade that is sister to populations of most southern mountains (e.g., Uluguru, Malundwe, Udzungwa) and Pemba Island (Blackburn & Measey, 2009). There is little genetic divergence between populations of *A. xenodactyloides* from the West and East Usambaras, but populations from South Pare are yet to be included in phylogeographic analyses.

***Arthroleptis* sp. ?nov.**

Records—**WEST USAMBARA**, CAS 200516–17 (Mazumbai FR II).

Remarks: These two specimens were collected in pitfall buckets in Mazumbai FR at an elevation of ca. 1400–1600 m. Both specimens are small; CAS 200516 and 200517 have snout–vent lengths of 13.9 and 15.5 mm, respectively. These frogs exhibit the typically smooth skin of *Arthroleptis*, but, unlike at least other *Arthroleptis* in the EAM, the skin of the body, head, and limbs is covered with many small, well-spaced spiny tubercles. Another notable feature is the supratympanic band, which overlies a small and near indistinct tympanum, is solid, and forms an elongate ventrally directed C with no spots trailing anterior or posterior from it. The inner metatarsal tubercle is small and ovoid, bordering on globose, and there are no supernumerary tubercles on the plantar surface. These specimens are clearly distinct morphologically from other *Arthroleptis* in the EAM and East Africa in general. However, both specimens are juveniles, or at least immature adults, and

FIG. 3. Photographs of some amphibians from the northwestern Eastern Arc Mountains; clockwise from top left, *Callulina stanleyi* (Chome FR), *Nectophrynoides vestergaardi* (Mazumbai FR), *Scolecomorphus* cf. *vittatus* (Kindoroko FR), and *Leptopelis* cf. *parkeri* (Chome FR).

we refrain from describing this taxon as a new species until more material becomes available.

***Leptopelis flavomaculatus* (Günther, 1864)**

RECORDS—**WEST USAMBARA**, FMNH 275635–36 (Ambangulu FR V).

***Leptopelis parkeri* Barbour and Loveridge, 1928**

RECORDS—**WEST USAMBARA**, BMNH 2005.1365–66 (Mazumbai FR II); CAS 168784–813 (Mazumbai FR II), 168814 (Baga II FR); FMNH 250483, 248025–26 (Ambangula FR III); MHNG 2620.097–098, 2687.065–066 (Mazumbai FR II); ZMUC R7737–84 (Mazumbai FR II); **SOUTH PARE**, MHNG 2640.074–75 (Chome FR I); MTSN 7550–55 (Chome FR VI).

REMARKS: The West Usambara material matches the description of *L. parkeri* (Barbour & Loveridge, 1928). All West Usambara FMNH specimens are females. The dorsum in FMNH 248025–26 is very darkly colored, whereas in FMNH 250483 it is pale yellow and almost white. South Pare material is noticeably different in terms of the coloration and patterning (see Fig. 3). The South Pare material might represent a previously unrecognized species of *Leptopelis*.

***Leptopelis vermiculatus* (Boulenger 1897)**

RECORDS—**WEST USAMBARA**, BMNH 1982.582 (Mazumbai FR IV), 1982.583–86 (Ambangulu FR VIII), 2005.1367–68 (Mazumbai FR II); CAS 161373 (Ambangulu FR II), 168813 (Mazumbai FR II); FMNH 275623 (Mazumbai FR III); MHNG 2620.091–93, 2687.071–72 (Mazumbai FR II); USNM 226810 (Ambangulu FR VIII); ZMUC R77385–90 (Mazumbai FR II).

Family Brevicipitidae

****Breviceps fichus* Channing and Minter, 2004**

RECORDS—**WEST USAMBARA**: *Call recorded, no specimen taken (1500 m, near the [Tanner's] house, close to Mazumbai FR, 2 December 2005—Alan Channing, pers. comm.).

REMARKS: Although no specimens have yet been collected, this record is a very significant extension because it would extend the known distribution of *Breviceps fichus* more than 400 km to the northeast (Channing & Minter, 2004; Channing & Howell, 2006). A record of *B. mossambicus* by Mertens (1937) was referred to *B. fichus* by Channing and Minter (2004) but then dropped from the distributional map of Channing and Howell (2006), suggesting that *B. fichus* is indeed restricted to the EAM.

Callulina

Recent work on the brevicipitid genus *Callulina* demonstrates that new faunal surveys and detailed taxonomic study can quickly change long-standing patterns of species diversity and biogeography. The first species of *Callulina* was described by Nieden (1911) based on material from Amani in the East Usambara and has since been identified from many localities throughout the EAM (Channing & Howell, 2006). More than 80 years later, a second *Callulina* species, *C. kisiwamsitu*, was described by de Sá et al. (2004). This description was based on material from the West Usambara and was quickly followed by descriptions of four more *Callulina* species, all from the northernmost EAM, by Loader et al. (2009, 2010). These recent taxonomic works quintupled the species diversity in the genus and provided the first hints that the northernmost EAM is a center of speciation in *Callulina*. Taken together, recent work on *Arthroleptis* and *Callulina* suggests that similar high levels of diversity may be found in other genera when given appropriate and detailed taxonomic study.

***Callulina kisiwamsitu* de Sá, Loader, and Channing, 2004**

Records—**WEST USAMBARA**, BMNH 1974.21–23 (Mazumbai FR II), 1982.588–89 (Mazumbai FR II), 1982.590–92 (Shume-Magamba FR I), 1986.595–99 (Mazumbai FR II), 2002.45–46 (Mazumbai FR II), 2002.47 (Ambangulu FR I); CAS 160078, 168806–09 (Mazumbai FR II), 168815–19 (Ambangulu FR II); MCZ A-13632–33, A-13635 (Philipshof), A-138534 (Mazumbai FR I); MHNG 2621.15–18 (Mazumbai FR II); ZMUC R0937–47 (Mazumbai FR II).

***Callulina laphami* Loader, Gower, Ngalason, and Menegon, 2010**

Records—**NORTH PARE**, BMNH 2002.37–41, 2005.951; CAS 225134–35 (Kindoroko FR); MTSN 7123, 8609, 8611–14, 8621–22, 8632, 8640–41, 8648, (Minja FR).

***Callulina shengena* Loader, Gower, Ngalason, and Menegon, 2010**

Records—**SOUTH PARE**, BMNH 2008.465-466 (Chome FR VI); FMNH 251849–52, 255881–82 (Chome FR V); MTSN 9285, 9288–90 (Chome FR VI).

***Callulina stanleyi* Loader, Gower, Ngalason, and Menegon, 2010**

Records—**SOUTH PARE**, BMNH 2000.207 (Chome FR I), 2008.467–68 (Chome FR II); FMNH 251381–84 (Chome FR IV); MTSN 7541–42, 7544, 7559 (Chome FR II).

Family Bufonidae
***Amietophrynus brauni* (Nieden, 1911)**

Records—**WEST USAMBARA**, FMNH 248051 (Ambangulu FR II), 248052 (Ambangulu FR V); MCZ A-12445 (Bumbuli), A-138458, A-138507, A-138516–19 (Ambangulu FR VII).

***Amietophrynus gutturalis* (Power, 1927)**

Records—**WEST USAMBARA**, MCZ A-12452–54 (Bumbuli), A-138524 (Ambangulu FR VI); **SOUTH PARE**, BMNH 2000.734 (Chome FR I), 2005.898 (Pare Forest); FMNH 251385–86 (Chome FR IV), 251446 (Gonja FR).

***Nectophrynoides vestergaardi* Menegon, Salvidio, and Loader, 2004**

Records—**WEST USAMBARA**, BMNH 1982.499–501, 1982.509–12, 1982.514–17 (Shume-Magamba FR I), 2005.1340 (West Usambara); CAS 161371 (Shume-Magamba FR I), 169381–82 (Baga II FR), 200518 (Mazumbai FR II); FMNH 251445, 248020–22, 250604–09 (Ambangulu FR IV); ZMUC R131228-48 (Mazumbai FR II).

Family Hyperoliidae
***Afrixalus fornasini* (Biaconi, 1849)**

Records—**WEST USAMBARA**, CAS 169250–52 (Mazumbai FR II).

***Afrixalus uluguruensis* (Barbour and Loveridge, 1928)**

Records—**WEST USAMBARA**, BMNH 1974.240–41 (Mazumbai FR, not found in the collection but identified by A. G. C. Grandison), 1982.567 (Mazumbai FR II), 2005.1334–35 (Mazumbai FR II); CAS 169266–74, 169937 (Mazumbai FR II); FMNH 276749, 276750, 278936 (Mazumbai FR I); MCZ A-13321 (Bumbuli); MHNG 2620.080–82 (Mazumbai FR II); ZMUC R77268–87 (Mazumbai FR II).

***Hyperolius argus* Peters, 1854**

Records—**WEST USAMBARA**, BMNH 1982.565 (Ambangulu FR VIII).

***Hyperolius mitchelli* Loveridge, 1953**

Records—**WEST USAMBARA**, FMNH 274532–36, 275025–29 (Ambangulu FR VI); **NORTH PARE**, MTSN 8643 (Kindoroko FR).

***Hyperolius* cf. *parkeri* Loveridge, 1933**

Records—**WEST USAMBARA**, FMNH 274550 (Ambangulu FR VI).

Remarks: This juvenile specimen was light green in life but is in a poor condition of preservation. DNA from the specimen was sequenced and demonstrates that it is conspecific with confirmed specimens of *Hyperolius parkeri* from Man'gula in the Udzungwa Mountains. Genetic data from this specimen was 1% divergent from that of positively identified specimens for the mitochondrial NADH dehydrogenase 2 (ND2) gene and two nuclear genes (pro-opiomelanocortin [POMC] and cellular myelocytomatosis c-myc; L. Lawson, unpubl. data). Molecular sequences are deposited in GenBank under the FMNH ID 274550.

***Hyperolius puncticulatus* (Pfeffer, 1893)**

Records—**WEST USAMBARA**, BMNH 1974.260–68, 1974.323–37 (Mazumbai FR II), 2005.1364 (Mazumbai FR II); CAS 169105–248 (Mazumbai FR II); FMNH 274526–30. LL18800–02, 18808–09, and 18811–13 are at UDSM to be catalogued (Mazumbai FR I), FMNH 274506–07, 274405, 274508–13. LL18824-18827 are at UDSM to be catalogued (Shume-Magamba FR II), FMNH 275001–10, 275011–15 (Ambangulu FR VI); MCZ A-13291, A-132675–85, A-13286–95 (Bumbuli); MHNG 2621.009–14, 2688.018 (Mazumbai FR II); ZMUC R77325–55 (Mazumbai FR II).

Hyperolius pusillus **(Cope, 1862)**

RECORDS—**WEST USAMBARA**, FMNH 248041 (Ambangulu FR IV).

Hyperolius tanneri **Schiøtz, 1982**

RECORDS—**WEST USAMBARA**, CAS 169263–65 (Mazumbai FR II); FMNH 274287–88 (Mazumbai FR I), 274289 (Shume-Magamba FR II); ZMUC R077356–72 (Mazumbai FR II).

Hyperolius glandicolor **Peters, 1878**

RECORDS—**SOUTH PARE**, BMNH 2000.735 (Chome FR I); **NORTH PARE**, MTSN 8635–36 (Kilomeni Mission).

Kassina maculata **(Duméril, 1853)**

RECORDS—**WEST USAMBARA**, BMNH 1974.401 (Mazumbai FR II).

Family Microhylidae
Hoplophryne **sp.**

RECORDS—**WEST USAMBARA**, FMNH 250472–75 (Ambangulu FR IV).

REMARKS: Three juvenile specimens (FMNH 250473–75; 11.8–14.0 mm snout–vent length) are tentatively identifiable to the genus *Hoplophryne* but show differences from other members of the genus (*H. rogersi* and *H. uluguruensis*; Barbour & Loveridge, 1928). FMNH 250472 is entered in the catalogue but has been returned to the donor institution (University of Dar es Salaam). Each of these specimens has long and gracile limbs. Furthermore, there are distinct and symmetrically arranged spines present on the dorsal surface; these spines are mainly concentrated posteriorly in FMNH 250475. Further assessment of these specimens will be required, but given the differences with described *Hoplophryne* species, these specimens likely represent a morphologically distinct and undescribed species.

Family Phrynobatrachidae
Phrynobatrachus krefftii **Boulenger, 1909**

RECORDS—**WEST USAMBARA**, BMNH 2005.1370–72 (Mazumbai FR II), 1974.64–95 (Mazumbai FR II); CAS 168727–83, 169380 (Mazumbai FR II); FMNH 272048 (Shume-Magambo II); MCZ A-12776–78 (Bumbuli), A-138286, A-138296–309, A-138455–57 (Mazumbai FR I), A-138310–15, A-138364, A-138551 (Ambangulu FR VI); MHNG 2621.019–020 (Mazumbai FR II).

REMARKS: FMNH 272048 is a juvenile specimen lacking the distinctive yellow throat of adult *P. krefftii*; thus, there is some uncertainty regarding its identity.

Phrynobatrachus natalensis **(Smith, 1849)**

RECORDS—**NORTH PARE**, MHNG 2624.073 (Kindoroko FR)

Phrynobatrachus **sp.**

RECORDS—**WEST USAMBARA**, BMNH 1974.158–69 (Mazumbai FR II).

REMARKS: The material was identified by Grandison as *P. minutus,* a species probably restricted to Ethiopia (B. M. Zimkus, pers. comm.). It resembles *P. ukingensis* in the presence of a light subtympanic band in most specimens, but the gular region is only lightly darkened. The presence of a clearly visible tympanum and slight but discernible expansion of digital tips into discs excludes this material from *P. schlefferi.*

Family Pipidae
Xenopus **cf.** *victorianus* **Ahl, 1924**

RECORDS—**WEST USAMBARA**, BMNH 1982.495 (Shume-Magamba FR I); MCZ A-12384–87 (Bumbuli).

REMARKS: There is doubt regarding the taxonomic status of *Xenopus* populations from the EAM. Specimens from the MCZ (A-12384–87; B. M. Zimkus, pers. comm.) reportedly have the following features: (1) claws present only on the first three toes and (2) a subocular tentacle less than half the diameter of the eye. Because of the relative length of the subocular tentacle, these specimens differ morphologically from *X. muelleri* (Kobel et al., 1996). While superficially resembling *X. victorianus,* the fifth toe of the West Usambara specimens is approximately the same length as the crus, whereas in *X. victorianus,* the fifth toe is somewhat longer than the crus (Kobel et al., 1996). Detailed taxonomic study will be required on *Xenopus* across the EAM to understand the status of each species. Because other montane regions in sub-Saharan Africa contain a number of endemic *Xenopus* species (e.g., Kobel et al., 1980; Loumont & Kobel, 1991; Evans et al., 2008), it would be unsurprising if this is similarly true for the EAM.

Family Ptychadenidae
Ptychadena anchietae **(Bocage, 1868)**

RECORDS—**WEST USAMBARA**, MCZ A-138527 (Ambangulu FR VI); **SOUTH PARE**, FMNH 251439–40 (Gonja FR), 251370–72 (Chome FR IV); MTSN 7547 (Chome FR II); **NORTH PARE**, MHNG 2624.066–067, 2624.070–73 (Kindoroko FR).

Family Pyxicephalidae
Amietia angolensis **(Bocage, 1866)**

RECORDS—**WEST USAMBARA**, BMNH 1974.132–44, 1982.558 (Mazumbai FR II); CAS 168828 (Handei Village Pond), 168719–26, 168804, 168830 (Mazumbai FR II); FMNH 248039 (Ambangulu FR IV); MCZ A-12661–65 (Bumbuli); **SOUTH PARE**, BMNH 2000.736 (Chome FR I); FMNH 251373–74 (Chome FR III), 251375–80 (Chome FR IV); MHNG 2619.094 (Chome FR I); MTSN 7548 (Chome FR II); **NORTH PARE**, MHNG 2624.068–69 (Kindoroko FR).

REMARKS: Several authors have suggested that there are probably cryptic species within those populations currently referred to as *Amietia angolensis* based on morphological grounds (Drewes & Vindum, 1994; Pickersgill, 2007). *Amietia angolensis* has a somewhat anomalously large elevational range (e.g., Poynton, 2003), which raises the possibility that lowland and highland populations are not conspecific. Although previous works have not dealt explicitly with material from the northern EAM, we leave open the possibility that cryptic species of *Amietia* might exist in the EAM.

Strongylopus fuelleborni **Nieden, 1911**

Records—**WEST USAMBARA**, BMNH 1929.6.1.6 (Philipshof); MCZ A-12715, A-12732–35 (Philipshof).

Remarks: There has been recent disagreement regarding the taxonomy of *Strongylopus* in the EAM and adjacent volcanic mountains of Mts. Kilimanjaro and Meru (Channing & Davenport, 2002; Poynton, 2004; Clarke & Poynton, 2005). The taxonomic and phylogenetic relationships of *Strongylopus* in the northern EAM to those of the volcanic mountains are an important area for future research.

Order Gymnophiona
Family Caeciliidae
***Boulengerula* cf. *boulengeri* Tornier, 1896**

Records—**WEST USAMBARA**, BMNH 2005.1343–48 (Lushoto), 2005.1349–56 (Ambangula FR I), 2005.1357–63 (Mazumbai FR II); CAS 168822 (Mazumbi FR II); ZMUC R361289, R361291–93 (uncertain locality – see below), 361393 (Mazumbai FR II).

Remarks: The existence of an undescribed new species from West Usambara has been suggested based on morphological and molecular data (Vestergaard, 1994; Channing & Howell, 2006; Loader et al., 2011). At least some West Usambara specimens referred to here as *B.* cf. *boulengeri* have more annuli and vertebrae than those from East Usambara. In addition, genetic distances between West and East Usambara samples provide some support for the suggestion of a new species (Loader et al., 2011). However, further detailed taxonomic study is required. There are uncertainties regarding the locality data for a series of specimens in Copenhagen collections (ZMUC-R 361291–93). This collection of *Boulengerula* material was made by M. Anderson, J. Rasmussen, and M. Vestergaard in East Usambara (Amani Nature Reserve) and West Usambara (Mazumbai FR) in consecutive days in September 1992. Field notes accompanying the amphibian material were lost and this has raised doubts about the exact provenance of these specimens.

Family Scolecomorphidae
***Scolecomorphus* cf. *vittatus* (Boulenger, 1895)**

Records—**WEST USAMBARA**, CAS 168810–11 (Mazumbai FR II), 168812 (Baga II FR); FMNH, 248043-46, 250532, 250589, 251437 (Ambangulu FR IV); MCZ A-12189 (Philipshof); ZMUC R0265, R361273, R361286, R361288, R0197 (Mazumbai FR II); **SOUTH PARE**, BMNH 2005.902–914 (Chome FR I); MTSN 7549 (Chome FR II); **NORTH PARE**, BMNH 1986.609 (Kifula Village, Ugweno), 2005.954–85 (Kindoroko FR); CAS 159945–64 (Kifula Village, Ugweno); MTSN 8619–20, 8631, 8633–34, 8637–39 (Kindoroko FR), 8642, 8644–45, 8647, 8649 (Minja FR); UMMZ 172066-7 (Kifula Village, Ugweno); USNM 226753 (Kifula Village, Ugweno).

Remarks: The diversity of scolecomorphid caecilians across the Usambara and Pare Mountains is currently being assessed (Loader, unpubl. data). It is likely that new species will be described from this material. Differences between populations in this region were implied in Nussbaum's (1985, pg. 30) review of material from North Pare: "Adults from the North Pare Mountains, to the northwest of the Usambara, have more extensive dark dorsal bands, which extend ventrolaterally past the midlateral line. The ventrolateral, light coloration is a duller cream."

Discussion

Table 1 summarizes the species for which records are known from the West Usambara, South Pare, and North Pare Mountains. The records presented here substantially increase the knowledge of species distributions in this East African biodiversity hotspot. In total, West Usambara has 33 species known (four endemic), South Pare 12 species (three endemic), and the North Pare eight species (one endemic). Our assessment was unable to confirm the presence of *Arthroleptis adolfifriederici* and *Petropedetes* [*Arthroleptides*] *martiensseni*, both recorded by Channing and Howell (2006). Until specimens can verify the presence of these species, it should be concluded that these are absent from the West Usambara. It should be noted that any comparisons with other Eastern Arc fragments should consider the complexity of species turnover between highland and lowland areas (Poynton et al., 2007). Some of the records given in our list include species that are usually treated as being part of the fauna of surrounding lowlands and are noted in Table 1 (footnote 3; e.g., *Amietophrynus gutturalis*). Therefore the highland fauna of the West Usambara and Pares is less species rich than indicated and would be reduced if some of the lowland species that penetrate highland forest habitats are excluded. Intensive sampling across the altitudinal distribution of species in these areas would be required before this could be adequately treated.

Patterns of species diversity across these mountains show a gradual southeast-to-northwest decline in numbers from the West Usambara to North Pare. This is also mirrored in the number of endemic species to these areas (see Table 1). This trend is more marked if species diversity in the East Usambara is also considered (Poynton et al., 2007). If the data from IUCN et al. (2009) are used to refine the species distribution maps of Channing and Howell (2006), then the following are sub-montane or montane species found in the East Usambara but apparently absent in the West Usambara or Pares: *Arthroleptis xenodactylus*, *Petropedetes* [*Arthroleptides*] *martiensseni*, *Breviceps mossambicus*, *Hyperolius spinigularis*, *Hoplophryne rogersi*, *Leptopelis barbouri*, *L. uluguruensis*, *Nectophrynoides tornieri*, *Parhoplophryne usambarica*, *Probreviceps macrodactylus*, and *Ptychadena oxyrhychus*. Notably, this list includes three genera (*Petropedetes*, *Parhoplophryne*, and *Probreviceps*) for which there are currently no records from the West Usambara or Pares. One likely reason for the differences in species richness and taxonomic diversity is the unequal sampling across these habitats, with most surveys focused historically in the East and West Usambara. If this is the major source of difference, then it suggests that more diversity remains to be discovered in the West Usambara and Pares. However, apart from the unequal surveying, other factors are likely to be significant in explaining the differences in amphibian diversity across the northwestern EAM. Forest area decreases sharply from West Usambara to North Pare (323, 139, and 26 km^2, respectively; Table 2), and this area effect likely contributes to differences in species richness (as supported by Burgess et al., 2007). The climate is also increasingly drier along this cline (Burgess et al., 2007), and therefore the suitability of habitats for amphibians is expected to be proportionately reduced. Other taxonomic groups (e.g., trees, birds, and mammals) also reveal similar relative differences between these areas, suggesting a common biogeographic pattern (Burgess et al., 2007). Although we suspect many other species await discovery, we predict that

TABLE 1. Species list for amphibians of the West Usambara and Pare Mountains.

	West Usambara	South Pare	North Pare
Anura			
Arthroleptidae			
Arthroleptis affinis	X		
Arthroleptis anotis		X[1]	
Arthroleptis fichika	X	X	X
Arthroleptis lombergi	X[2]		
Arthroleptis stenodactylus	X	X	
Arthroleptis tanneri	X[1]		
Arthroleptis xenodactyloides	X	X	
Arthroleptis sp. ?nov.	X		
Leptopelis flavomaculatus[3]	X		
Leptopelis parkeri	X	X	
Leptopelis vermiculatus	X		
Brevicipitidae			
Breviceps fichus[3,4]	X		
Callulina kisiwamsitu	X[1]		
Callulina laphami			X[1]
Callulina shengena		X[1]	
Callulina stanleyi		X[1]	
Bufonidae			
Amietophrynus brauni	X		
Amietophrynus gutturalis[3]	X	X	
Nectophrynoides vestergaardi	X[1]		
Hyperoliidae			
Afrixalus fornasini[3]	X		
Afrixalus ulugurnensis	X		
Hyperolius argus[3]	X		
Hyperolius glandicolor[3]		X	X
Hyperolius mitchelli[3]	X		X
Hyperolius parkeri[3]	X		
Hyperolius puncticulatus	X		
Hyperolius pusillus[3]	X		
Hyperolius tanneri	X[1]		
Kassina maculata[3]	X		
Microhylidae			
Hoplophryne sp.	X		
Phrynobatrachidae			
Phrynobatrachus krefftii	X		
Phrynobatrachus natalensis[3]			X
Phrynobatrachus sp.	X		
Pipidae			
Xenopus victorianus[3]	X		
Ptychadenidae			
Ptychadena anchietae[3]	X	X	X
Pyxicephalidae			
Amietia angolensis[3]	X	X	X
Strongylopus fuelleborni	X		
Gymonphiona			
Caeciliidae			
Boulengerula boulengeri	X		
Scolecomorphidae			
Scolecomorphus cf. *vittatus*	X	X	X
Total (total endemic species)	33 (4)	12 (3)	8 (1)

[1] Endemic to this single fragment.

[2] Questionable status.

[3] Associated with lowland fauna.

[4] Not verified by a specimen.

differences between these areas might remain roughly the same when future studies survey these Eastern Arc forest fragments.

A general comparison of the amphibian communities reveals that the West Usambara and South Pare Mountains show similar species composition. A total of eight species are shared between West Usambara and South Pare, more than the five species shared between the Pares or the four among West Usambara and North Pare. Future taxonomic assessment of particular species (e.g., *Arthroleptis fichika, Scolecomorphus* cf. *vittatus*) is likely to further reduce the proportion of taxa shared between these mountains. The close biotic relationship between populations in the West Usambara and South Pare Mountains (and other northern Eastern Arc mountains such as the Taita or Shimba Hills) appears to be a

Table 2. Estimates of forest area, and elevational coverage for the East and West Usambara and South and North Pare Mountains.

	East Usambara	West Usambara	South Pare	North Pare
Forest area (km^2) according to Newmark (2002)[1]	413	547	333	151
Forest area (km^2) according to various other published sources (see notes)[1]	450	220	211	25
Forest area (km^2) according to standardized analysis of satellite imagery[1]	263	319	138	27
Estimate of forest area (km^2)[2]	263	323	139	26
Estimates of % change in forest cover across the Northern Eastern Arc Mountain blocks (Paleo. – 2000)[2]	−68.3	−86.3	−87.2	−92
Forest elevational coverage[1]	130–1506	1200–2200	820–2463	1300–2113

[1] Taken from Burgess et al., 2007.

[2] Taken from Hall et al., 2009.

pattern repeated in molecular studies that have been conducted across these areas (Bowie et al., 2004, 2006; Fjeldså et al., 2006; Kahindo et al., 2007; Blackburn, 2009a; Blackburn & Measey, 2009; Loader et al., 2009, 2010). Future molecular studies designed explicitly to test this pattern are required to determine the extent of this shared biogeography.

The diversity of amphibians in the Usambara and Pares highlights the conservation importance of these areas. Numerous endemic species from single forest fragments are known from these areas, including species of conservation concern (Loader et al., 2010). Remarkably, two *Callulina* species, stratified by elevation, are known in the South Pare in the Chome Forest Reserve (Loader et al., 2010). In addition to the new *Arthroleptis* species described here, these forest-restricted amphibian species, and the forest habitats they occupy, deserve conservation attention.

Land use changes in the Usambara Mountains have occurred over a prolonged period (Newmark, 2002). Early Iron Age sites demonstrate that lower portions of the montane zone (>1200 m) were occupied in West Usambara at least by the third century C.E. (Schmidt, 1988); use of forest products at these sites is clearly evident via the wood charcoal used in iron-smelting furnaces. In this and later time periods, mountain farmers in the Usambaras settled in and farmed montane and sub-montane zones where they cultivated a wide variety of crops, such as bananas (*Musa* spp.) that arrived because of trade with coastal sites integrated into oceanic trade routes (reviewed in Conte, 2004). Although the extent of forest present 2000 years ago was undoubtedly reduced in size before the nineteenth century, some of the most dramatic short-term changes in forest cover came in the late nineteenth and early twentieth centuries with the advent of German and, subsequently, British occupation (Conte, 2004). In the first half of the twentieth century, large amounts of forest were removed in the Usambara Mountains in order to plant economic crops on supposedly fertile soils (Conte, 2004). According to Hall et al. (2009), during the past 2000 years, the West Usambara have suffered a reduction in forest cover by 86%, the South Pare by 87%, and the North Pare by 92%. However, it should be noted that these recent comparisons by Hall et al. (2009) lump all deforestation from 2000 years ago to 1955 in the same time category, which makes it difficult to evaluate the degree of change that preceded the implementation of colonial forest management practices. Today there remains a strong concern for the conservation of the forest habitats in West Usambara (Goodman et al., 1995) and Pares (Hall et al., 2009), which have had dramatic historical reductions in size and for which our knowledge of the fauna is still woefully incomplete.

Gazetteer

North Pare Mountains

Kifula, Ugweno [3°37′30″S, 37°40′00″E].
Kindoroko FR [3°43′43.5″S, 37°39′16.1″E].
Minja FR [3°44′55.96″S, 37°38′47.09″E].
Kilomeni Mission [3°45′59.87″S, 37°38′59.73″E].

South Pare Mountains

Chome FR I [4°18′S, 37°53′E, 1800 m].
Chome FR II [4°19′41.382″S, 37°59′44.262″E].
Chome FR III, edge Chome FR, 5.5 km S Bombo (by air), near Kunza Village [4°19′S, 38°00′E, 1100 m].
Chome FR IV, 7 km S Bombo (by air) [4°20′S, 38°00′E, 1100 m].
Chome FR V, 3 km E, 0.7 km N Mhero [4°17′S, 37°55′40″E, 2000 m].
Chome FR VI, Shengena [4°17′42.907″S, 37°56′18.612″E].
Gonja FR, Higililu River [4°16′S, 38°02′E, 550 m].
Nakombo River [4°09′S, 37°56′E].
Pare Forest [4°09′S, 37°50′E].

West Usambara Mountains

West Usambara [4°43′S, 38°15′E, 1860 m]
Ambangulu FR I, BM [5°3′S, 38°24′E, 1250 m].
Ambangulu FR II, Tea Estate [5°4′S, 38°25′E, 1300 m].
Ambangulu FR III, Tea Estate, 14.5 km NW Korogwe [5°3′S, 38°23′E, 1250 m].
Ambangulu FR IV, Tea Estate, 12.5 km NW Korogwe [5°4′S, 38°25′E].
Ambangulu FR V, Tea Estate [5°5′S, 38°26′E, 1200 m].
Ambangulu FR VI, Tea Estate, 1102 m [5°3.266′S, 38°22.672′E].
Ambangulu FR VII, Tea Estate, 1252 m [5°3′57″S, 38°24′0″E].

Ambangulu FR VIII, Tea Estate [5°5′S, 38°26′E, 1200 m; Howell and Stuart, 1984].
Baga II FR [4°48′S, 38°27′E].
Balangai FR [4°55′59″S, 38°36′60″E].
Bumbuli [4°52′00″S, 38°27′60″E].
Handei Village Pond [unknown co-ordinates]
Lushoto [unknown co-ordinates].
Mazumbai FR I [4°49′45″S, 38°30′46″E].
Mazumbai FR II [4°49′S, 38°29.5′E].
Mazumbai FR III [4°48′S, 38°30′E, 1450 m].
Mazumbai FR IV [4°48′S, 38°29′E, 1500 m; Howell and Stuart, 1984].
Mombo [4°54′50″S, 38°17′29″E].
Philipshof [4°45′00″S, 38°30′00″E].
Shume-Magamba FR I [4°40′S, 38°10′E, 2134 m].
Shume-Magamba FR II [4°43′34″S, 38°14′58″E, 1920 m]
Shume-Magamba FR III edge [4°44′52″S, 38°17′51″E, 1642 m]

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Chapter 8

Herpetofauna of Montane Areas of Tanzania. 4. Amphibians and Reptiles of Mahenge Mountains, with Comments on Biogeography, Diversity, and Conservation

Michele Menegon[1,2], Claire Bracebridge[2,3], Nisha Owen[4,5], and Simon P. Loader[6]

[1]*Tropical Biodiversity Section, Museo Tridentino di Scienze Naturali, Via Calepina 14, I–38100, Trento, Italy*
[2]*Department of Environmental & Geographical Sciences, Manchester Metropolitan University, Manchester, United Kingdom*
[3]*Wildlife Conservation Society, P.O. Box 1475, Mbeya, Tanzania*
[4]*Frontier Tanzania Forest Research Program, P.O. Box 9473, Dar es Salaam, Tanzania*
[5]*Society for Environmental Exploration/Frontier, London, United Kingdom*
[6]*Institute of Biogeography, University of Basel, Basel, Switzerland*

Abstract

The Mahenge Mountains are located in the Eastern Arc Mountains, part of a global biodiversity hotspot. Few amphibian and reptile surveys have been conducted in this area, with only one study of the submontane forest zone. This previous study revealed a characteristic endemic Eastern Arc amphibian and reptile forest fauna. New studies outlined here extend the sampling time considerably and the geographical coverage (including Mselezi Forest Reserve). These studies reveal a remarkable diversity of amphibians and reptiles increasing known faunal diversity considerably, including several putative new species that await further taxonomic verification. Biogeographical analyses using Bray-Curtis indices show Mahenge clusters with the geographically close Udzungwa Mountains and Southern Highlands (non–Eastern Arc highland fragment including Mt. Rungwe). This clustering of areas suggests an interesting biogeographical history and deserves special attention in the future. In light of the remarkable amphibian and reptile diversity, conservation of Mahenge habitats, in particular Sali Forest Reserve, is desperately required.

Introduction

The Mahenge Mountains form the southernmost part of the Eastern Arc Mountains (EAM), a recognized biodiversity hotspot (Myers et al., 2000). These mountains constitute several relatively poorly known forest fragments. To the west, the Mahenge Mountains are bordered by the Kilombero floodplain, separating them from the Udzungwa Mountain range. To the south the mountains form an almost continuous mountain block with the Mbarika Mountains, which are linked to the Livingstone Mountains and the Southern Highlands north of Lake Nyasa (Fig. 1).

The Mahenge Mountains are estimated to have lost 89% of their original forest cover (Newmark, 1998), although the rate of loss appears to have declined in the last few decades. However, most of the forest fragments that remain in the Mahenge Mountains are small and heavily encroached upon due to accessibility and proximity to humans (Mbilini & Kashaigili, 2005). The forests consist of a number of fragments with different degrees of disturbance and natural habitats remaining. However, the two southernmost forests, Sali and Muhulu Forest Reserves (FR), have remained relatively intact due to their isolation.

Knowledge of the distribution of species across the fragmented forests of Mahenge is very incomplete. Currently, assessments of the Mahenge Mountains indicate that the area has one endemic vertebrate species (Mariaux & Tilbury, 2006), 11 Eastern Arc near-endemic vertebrates, and five Eastern Arc near-endemic trees (Burgess et al., 2007). Because of the relatively low species diversity and endemism in the Mahenge Mountains, it is ranked low on the list of conservation priorities for the Eastern Arc (Critical Ecosystem Partnership Fund, 2005).

Historically, biological research in the Mahenge Mountains has been limited. Early exploration surveyed the herpetofauna and small mammals in the 1960s in Mahenge (Rees, 1964; with material examined and described by Poynton, 1977, 1991, 2003). Parts of the Mahenge Mountains were the focus of research by Frontier Tanzania, including surveys of amphibians and reptiles. Research focused on Mahenge Scarp Forest Reserve, Nawenge Forest Reserve, and Nambiga Forest Reserve (outlined in the reports of Frontier Tanzania, 2001–2004). However, these areas constitute mainly lowland habitats (Hinde et al., 2001), including miombo-type habitats, and not submontane or montane forest habitats. A botanical appraisal of catchment forest reserves (Lovett & Pócs, 1993) provided information on the flora of the region and each

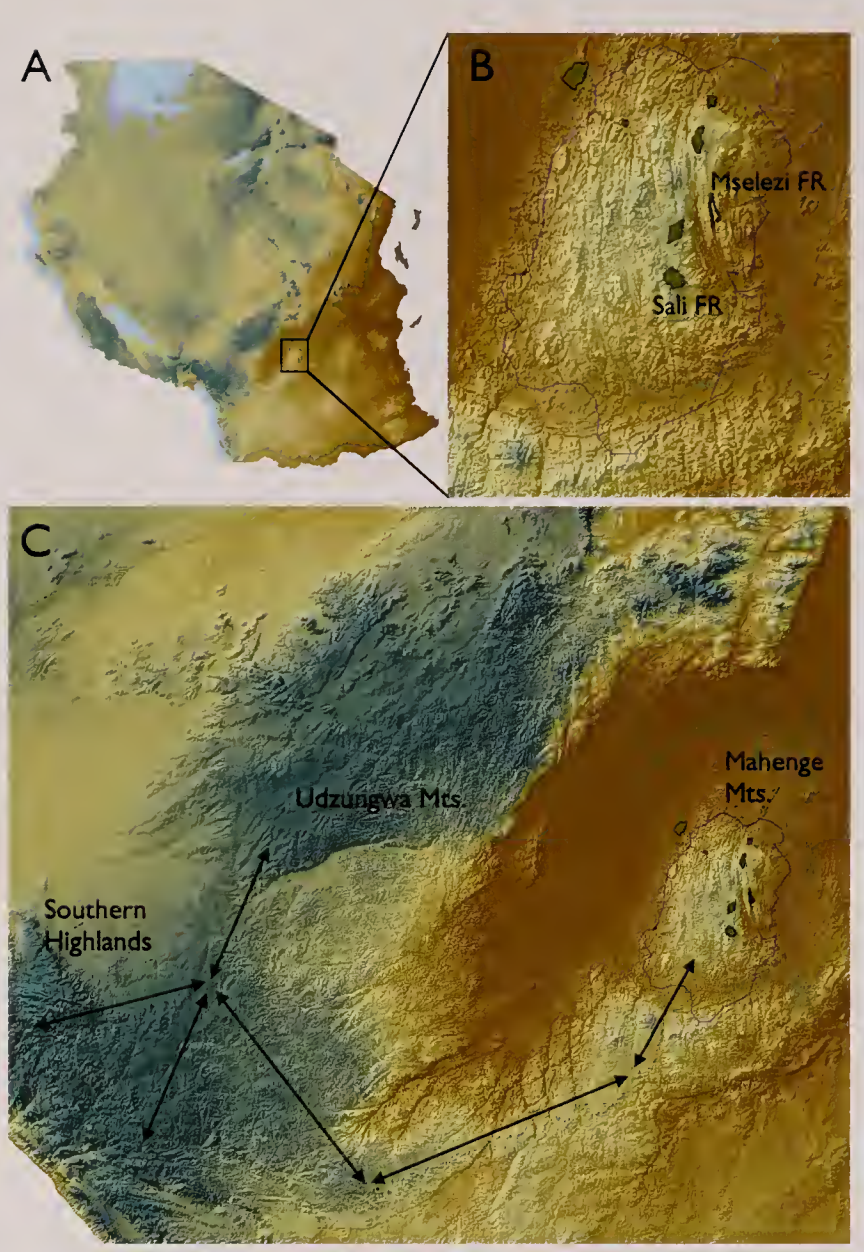

FIG. 1. Map of Tanzania showing (**A**) the position of the Mahenge Mountains within the Eastern Arc Mountains. (**B**) Position of surveyed forest fragments within the Mahenge Mountains landscape. (**C**) Possible faunal dispersal routes across Udzungwa, Southern Highlands, and Mahenge Mountains.

forest reserve. Several plant species with restricted distributions have been recorded (Lovett & Pócs, 1993). These include two endemic *Impatiens* spp. and the Eastern Arc endemic *Allanblackia stuhlmannii* (Lovett & Pócs, 1993). The presence of such species links the forest habitats to the biologically rich forests of the rest of the Eastern Arc Mountains.

Sali FR was the subject of one previous focused survey of the herpetofauna, updating the species inventory for amphibians and chameleons (Loader et al., 2004). The three-day survey provided the first glimpse of the affinities to other Eastern Arc submontane/montane forest herpetological assemblages. The presence of particular species strongly suggested Eastern Arc affinities, including *Scolecomorphus kirkii, Petropedetes yakusini, Leptopelis vermiculatus, Nectophrynoides tornieri,* and *Afrixalus uluguruensis*. Overall, given the lack of surveys in Mahenge, new field research continues to be required to make a proper assessment of the diversity of amphibians and reptiles in this Eastern Arc Mountain fragment.

This paper documents surveys recently conducted in Mahenge Mountains across two separate forest reserves. The surveys constitute the most intensive survey in this region and forest habitat, totaling 59 survey days. The work builds considerably on the three-day survey of Loader et al. (2004), which is the only known survey restricted to submontane forest habitats in the region.

Methodology

Study Area

The Mahenge Mountains are an Eastern Arc outlier of small, biologically poorly known forest patches. Covering 2,802.29 km^2, they are located at 8°37′–8°38′S and 36°42′–36°44′E, and rise from 460 to 1500 m above sea level (masl). To the west, the Mahenge Mountains are bordered by the Kilombero floodplain that separates them from the Udzungwa Mountain range and the Southern Highlands, and to the south, the Mahenge Mountains form a continuous series of ridges with the Mbarika Mountains, which are attached to the great mountain ranges north of Lake Nyasa. The forest fragments investigated are Sali and Mselezi Forest Reserves, both located in Ulanga District in Morogoro Region (Table 1; Fig. 1).

Field Survey Methods

Several techniques were used to collect amphibians and reptiles. Pitfall bucket lines were constructed at each field site for eight days to sample terrestrial herpetofauna, with two sites in Sali FR and one site in Mselezi FR. Three 50-m lines of drift fencing with 33 pitfall buckets were used for a total period of 792 trap-nights. Pitfalls were checked both in the morning and evening, with specimens collected from the buckets. Visual Encounter Surveys (VESs) of a total duration of 96 man-hours were used to sample quantitatively amphibians and reptiles through both quadrats and transects. VESs sample diurnal fossorial, arboreal, and water-associated species. Nocturnal acoustic monitoring techniques were used to detect the frog species. Furthermore, opportunistic sampling was made of all taxa throughout the survey. Material collected is listed in Appendix 1 by K. M. Howell collector numbers. The surveys were conducted between 12 Oct and 29 Nov 2005 in Sali FR and 25 Nov and 9 Dec 2005 in Mselezi FR. The taxonomy largely follows that of Frost et al. (2006). Tables 2 and 3 give the list of species for the two forest reserves surveyed.

The species collected were identified on the grounds of morphological, molecular, and bioacoustic analysis and through comparison with material held in the herpetological collections of the University of Dar es Salaam, Tanzania; the Natural Sciences Museum of Trento, Italy; and the Natural History Museum, London, United Kingdom, and are deposited in the Natural Sciences Museum of Trento. Molecular analyses were carried out at the Institute of Biogeography of the University of Basel, Switzerland. Analysis of similarity was performed with the software PAST—Palaeontological Statistics. A dendrogram was constructed based on a matrix of endemic and near-endemic Eastern Arc Mountain amphibian and reptile species by site, using the Bray–Curtis (Sørensen) similarity index.

Results

Species Diversity and Endemism

Tables 1 and 2 list the species recorded for the Mahenge Mountains across the two fragments surveyed in this study,

TABLE 1. History and geography of two Forest Reserves in the Mahenge Mountains. Information from Lovett and Pócs (1993) with updates from observations during the Frontier-Tanzania survey of Forest Reserves in the Mahenge Mountains (Frontier-Tanzania, 2004–2005).

	Sali FR	Mselezi FR
Year of establishment	1954	1954
Coordinates	8°54′–8°57′S, 36°37′–36°41′E	8°46′S, 36°43′E
Size (ha)	1890	2245
Altitude (masl)	1050–1500	500–900
Rainfall (mm/year)	1700	1500
Vegetation type	Primary submontane and montane forest; dry grassland, wetlands, rocky outcrops	Riverine lowland forest along the stream in the valley bottom; semi-evergreen drier lowland forest

and Figure 2 illustrates some of these taxa. The Mahenge Mountain herpetofauna, based on previous works (Hinde et al., 2001; Loader et al., 2004) and on the results presented here, comprises at least 41 species of amphibians in 13 families and 25 species of reptiles in eight families. The present study recorded seven amphibian taxa and one reptile taxon that are sufficiently distinct from the other known taxa that they may be considered new species based on the available data. Furthermore, the taxonomic status of all the species collected during the surveys has been assessed in the context of more extensive work on the genera, involving molecular, osteological, bioacoustic, and morphological analysis conducted from 2005 to date (S. Loader, unpubl. data; M. Menegon, unpubl. data; J. Poynton, unpubl. data). Specific determination is still in doubt for several taxa and will require further taxonomic work over the coming years, but all new putative species have minimally shown distinct genetic divergence (>3% difference using mitochondrial markers). For several putative species there is often supporting evidence for distinctiveness based on either vocalization and morphology or both. A similar case is shown in the Nguru Mountains (Menegon et al., 2008), and new species continue to be described from this area (e.g., Blackburn, 2008; Poynton et al. 2008; Loader et al., 2010).

Faunal composition includes typical elements of the Tanzanian lowlands, due to the close proximity to the Kilombero River valley (e.g., *Hyperolius tuberilinguis*, *Pyxyicephalus edulis*, *Phrynomantis bifasciatus*), and a majority of forest and highlands elements showing a strong link with the other forested areas in the Eastern Arc Mountains (e.g., species belonging to the genera *Callulina, Hoplophryne, Petropedetes, Probreviceps,* and *Nectophrynoides*). These EAM endemic or near-endemic amphibian genera are all represented by putative new species, highlighting the taxonomic distinctiveness of the Mahenge highland herpetofauna and further stressing the need for continued taxonomic assessment.

The forest-associated reptile assemblage is also distinctive, as exhibited in amphibians. A few putative new species are likely endemic to the Mahenge Mountains. A single female of the forest chameleon genus *Kinyongia* was collected, and it appears to be a distinctive species, closely related to the *K. oxyrhina* (Krystal Tolley, pers. comm.). *Kinyongia oxyrhina* is a species widely distributed across several of the Eastern Arc Mountain blocks, including Udzungwa, Uluguru, Nguu, Nguru, and Rubeho (Krystal Tolley, pers. comm.; Menegon, unpubl. data). The forest gecko *Cnemaspis* sp. is another putative endemic species new to science (Bauer & Menegon, in prep.). The Mahenge endemic dwarf chameleon *Rhampholeon beraduccii* collected and described from the previous survey in Sali FR already suggested the distinctiveness of the Mahenge reptile fauna. *Rhampholeon beraduccii* was again collected in the surveys outlined here. Other enigmatic findings are shown by the collection of two snake species. One specimen is tentatively identified as *Xyeledontophis* cf. *uluguruensis*, a poorly known species described from the Uluguru Mountains (Broadley and Wallach, 2002) and recently recorded in the Nguru Mountains (Menegon et al., 2008). Another interesting record is the burrowing asp *Atractaspis aterrima*, a Guineo-Congolian species, known also from a few localities within the Eastern Arc (Spawls et al., 2004; Menegon et al., 2008). Like amphibians, the occurrence of coastal/lowland elements is due to the close proximity of the Kilombero Valley, which contains lowland species and links to coastal areas along the Kilombero river valley (e.g., *Rieppeleon brevicaudatus*, *Dendroaspis angusticeps*, *Naja melanoleuca*).

Zoogeographical Patterns

Bray–Curtis Similarity Index values were computed for each Eastern Arc mountain fragment using non-transformed amphibian and reptile species occurrence data, based on Burgess et al. (2007), updated by recent publications (Blackburn, 2009), and unpublished data by the authors (Fig. 3). The pattern obtained shows an interesting clustering of sites reflecting similarities in species assemblages, which in general can be correlated to geographic proximity. The Taita Hills are separated from all the other sites, probably because of the paucity of Eastern Arc endemic and near-endemic species. The northernmost Tanzanian sites (North and South Pare Mountains) cluster together and are distinct from all other EAM blocks. The Pare and Taita differences reflect the distinctiveness of these assemblages (e.g., Müller et al., 2005; Loader et al. 2009, 2010). These results contrast with comparisons of amphibians given in Loader et al. (this volume) that identified closer links between West Usambara and South Pare to the exclusion of the North Pare Mountains. Clearly the biogeographical history of these areas remains uncertain and requires further detailed analyses using appropriate methodologies (e.g., historical biogeographical approaches).

Three other clusters are identified in the dendrograms constructed using the Bray–Curtis Similarity Index: (1) a cluster that includes the north-central Eastern Arc fragments (East and West Usambara, Nguru, and Uluguru); interestingly, the East and West Usambara do not form a single grouping; (2) the Central Eastern Arc region (Malundwe, Nguu, Rubeho, and Ukaguru), areas with relatively low species diversity but poorly surveyed; and (3) a southern Eastern Arc cluster, (Udzungwa, Mahenge, and Rungwe [Southern Highlands], which is a non–Eastern Arc Mountain fragment). We note the close relationship shared between Udzungwa and Rungwe, to the exclusion of Mahenge.

TABLE 2. List of the amphibians of Mahenge Mountains.

Taxon	Sali FR	Mselezi FR	Data source (if not present study)
Arthroleptidae			
Arthroleptis lonnbergi	X	X	
Arthroleptis sp. 1	X	X	
Arthroleptis cf. *reichei*	X	X	
Arthroleptis xenodactyloides	X	X	
Leptopelis flavomaculatus	X		
Leptopelis uluguruensis	X		
Leptopelis vermiculatus	X		
Bufonidae			
Amietophrynus gutturalis			Loader et al., 2004
Amietophrynus maculatus			Loader et al., 2004
Nectophrynoides cf. *tornieri*	X		
Nectophrynoides sp. 1	X		
Nectophrynoides sp. 2	X		
Mertensophryne loveridgei		X	
Hemisotidae			
Hemisus marmoratus			Loader et al., 2004
Hyperolidae			
Afrixalus cf. *uluguruensis*	X		
Afrixalus fornasinii	X	X	
Afrixalus sp. 1	X		
Afrixalus sp. (cf. brachycnemis)			Loader et al., 2004
Hyperolius puncticulatus	X		
Hyperolius mitchelli			Loader et al., 2004
Hyperolius tuberilinguis			Loader et al., 2004
Hyperolius nasutus			Loader et al., 2004
Hyperolius sp. 1	X		
Kassina senegalensis			Loader et al., 2004
Microhylidae			
Hoplophryne sp.	X		
Phrynomantis bifasciatus			Loader et al., 2004
Brevicipitidae			
Callulina sp.	X		
Probreviceps cf. *rungwensis*	X		
Breviceps mossambicus			Loader et al., 2004
Spelaeophryne metheneri	X	X	
Petropedetidae			
Petropedetes sp.	X	X	
Phrynobatrachidae			
Phrynobatrachus acridoides		X	
Phrynobatrachus natalensis	X	X	
Phrynobatrachus uzungwensis	X		
Ptychadenidae			
Ptychadena anchietae		X	
Pyxicephalidae			
Amietia angolensis	X		
Pyxicephalus edulis			Loader et al., 2004
Pipidae			
Xenopus muelleri			Loader et al., 2004
Rhacophoridae			
Chiromantis xerampelina			Loader et al., 2004
Scolecomorphidae			
Scolecomorphus cf. *kirkii*	X		Loader et al., 2004

Discussion

Loader et al. (2004) outlined the differentiation of the highland herpetofauna of the Mahenge Mountains from the lowland area of the Kilombero Valley. The assessment, based on amphibians, showed high turnover patterns across this transect, with the presence of key species only in the montane zone. These key species were associated with other highland areas of the Eastern Arc. The study by Loader et al. (2004) supported what was well understood by geologists and some biologists previously (Lovett & Pócs, 1993); these Eastern Arc highland regions have a shared biogeographic history, as implied by the species they share. However, based on the rather limited sampling and taxonomic understanding, no endemics

TABLE 3. List of the reptiles of Mahenge Mountains.

Taxon	Sali FR	Mselezi FR	Data source (if not present study)
Gekkonidae			
Cnemaspis sp.	X	X	Loader et al., 2004[1]
Chamaeleonidae			
Chamaeleo dilepis	X		
Trioceros melleri	X		
Kinyongia cf. *oxyrhina*	X		
Rhampholeon beraduccii	X		Loader et al., 2004[1]
Rieppeleon brevicaudatus	X	X	Loader et al., 2004
Scincidae			
Melanospes cf. *loveridgei*	X	X	
Trachylepis striata	X	X	
Typhlopidae			
Rhinotyphlops mucruso	X		Loader et al., 2004
Colubridae			
Crotaphopeltis tornieri	X		
Crotaphopeltis hotamboeia	X		
Dasypeltis medici		X	
Lycodonomorphus whitei	X		
Philothamnus hoplogaster	X		
Philothamnus angolensis	X		
Philothamnus semivariegatus		X	
Psammophis orientalis	X		
Natriciteres sylvatica	X		
Thelotornis mossambicanus	X	X	
Xyelodontophis cf. *uluguruensis*	X		
Lamprophiidae			
Lamprophis cf. *fuliginosus*	X		
Atractaspis aterrima	X		
Elapidae			
Dendroaspis angusticeps		X	
Naja melanoleuca	X	X	
Viperidae			
Causus defilippii	X		

[1] Data source shows different taxonomic identity.

were identified, but rather, species with seemingly larger distributions across southern Eastern Arc areas (e.g., *Scolecomorphus kirkii*) and in some cases potentially northern areas (e.g., *Nectophrynoides tornieri*). Closer scrutiny of the region was encouraged despite Mahenge's relatively low diversity. Mahenge's apparent close relationship to other hyperdiverse Eastern Arc areas suggested it might also be diverse, but lack of research had precluded a proper assessment.

In this study, we outlined new discoveries revealing a remarkable diversity of amphibians and reptiles of the Mahenge Mountains. Numerous putative new species have been identified but await further taxonomic work. These results improve substantially our understanding of the Mahenge Mountain herpetofauna. Surveys across a wider geographical area in Mahenge have identified putative new endemic species belonging to characteristic endemic Eastern Arc genera. The only previous survey conducted in this area (Loader et al., 2004), above 850 m in Sali FR, documented only seven montane Eastern Arc endemics or near-endemic species: *Scolecomorphus kirkii, Nectophrynoides tornieri, Speleaeophryne methneri, Petropedetes yakusini, Leptopelis vermiculatus, Afrixalus uluguruensis,* and *Hyperolius puncticulatus.* This study increased the total numbers substantially to 41 species, with radiations of putative endemic species belonging to genera previously recorded (e.g., *Nectophrynoides,* three species; *Leptopelis,* two species; *Afrixalus,* two species; *Arthroleptis,* two species). In addition, genera previously not recorded for this area include *Callulina, Hoplophryne,* and *Probreviceps.* Overall the increase in species diversity is remarkable and requires that remaining forest reserves in these regions to be assessed to understand how widely distributed these species are.

The documented diversity further exemplifies the hyperdiverse Eastern Arc amphibian fauna. Recent surveys, including those documented in this volume (Lawson & Moyer, 2008; Menegon et al., 2008; Loader et al., 2010), have started to establish that, beyond the well-surveyed forests (Uluguru, Udzungwa, and Usambara), areas previously considered less diverse often contain highly diverse assemblages after more extensive surveys are conducted. Surveys across all the fragmented forest areas of the Eastern Arc Mountains are required before anything can be presumed about species diversity.

The reptile fauna, even more poorly understood, is also a comparatively diverse assemblage in Mahenge. Prior to this study, only seven taxa were recorded; our surveys raised this total to 24 species, including one recently described endemic species (*Rhampholeon beraduccii*; Mariaux & Tilbury, 2006). Several reptiles are recorded as being putative new species, which await taxonomic verification (*Kinyongia* cf. *oxyrhina, Melanoseps* cf. *loveridgei, Crotaphopeltis* cf. *tornieri, Xyele-*

FIG. 2. Left column, descending: *Probreviceps* cf. *rungwensis*, *Callulina* sp., *Nectophrynoides* sp.; right column, descending: *Kinyongia* cf. *oxyrhina*, *Rhampholeon beraduccii*, *Cnemaspis* sp.

dontophis sp., and *Cnemaspis* sp.). The surveys also include the first records in this mountain fragment of the following genera: *Atractaspis*, *Kinyongia, Melanoseps, Crotaphopeltis,* and *Xyeledontophis*. This addition to the number of known reptile species in the area suggests that the region is both diverse with species characteristic of the Eastern Arc and contains numerous endemic species.

The presence of several Eastern Arc endemic or near-endemic genera and species suggests a strong link between the Mahenge Mountains and other EAM forested areas. Mahenge Mountains are geographically adjacent to the Udzungwa Mountains, and this proximity is also reflected in the close biogeographical relationships (see Fig. 3). Between these two areas is the deep and wide Kilombero Valley, which currently acts as a barrier to species dispersal. Evidence of this potential barrier has been provisionally outlined in the genetic differences exhibited by populations on either side of the Kilombero Valley. For example, populations of *Kinyongia oxyrhina* in Mahenge and Udzungwa show sufficient genetic differentiation to suggest long-term separation (Krystal Tolley, pers. comm.).

To the south, where the Mahenge Mountains are joined to the Southern Highlands by the Mbarika Mountains, dispersal might have also occurred across this southwestern corridor.

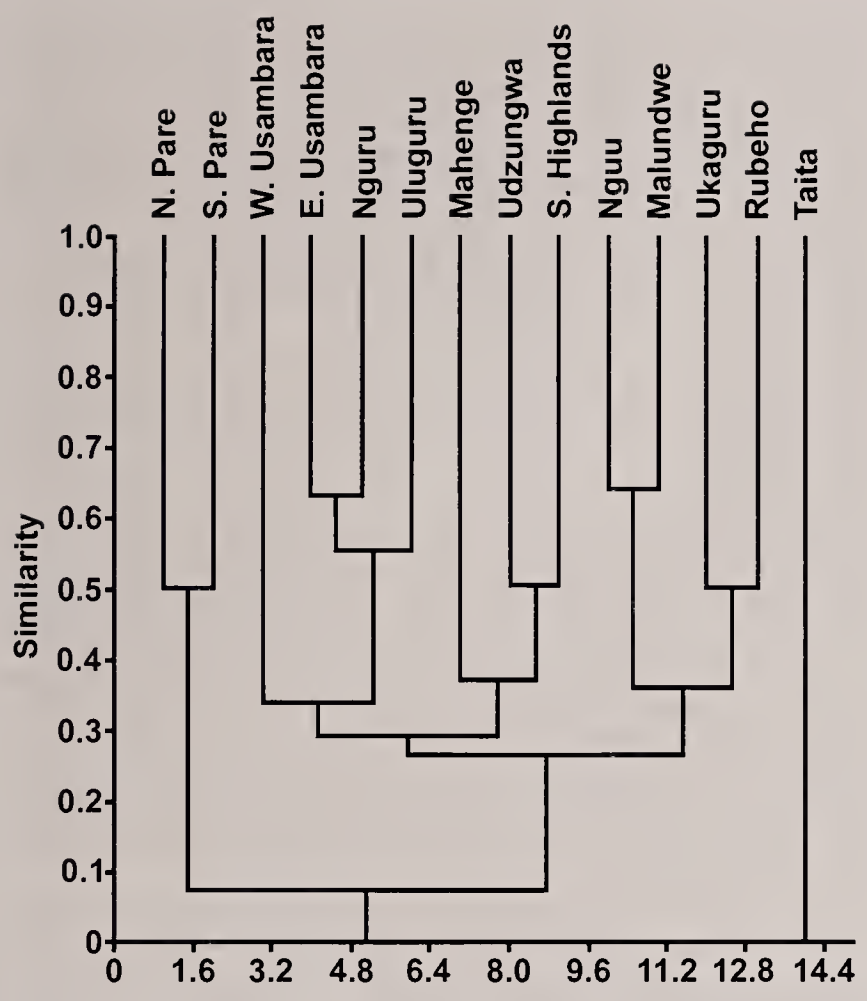

FIG. 3. Dendrogram based on a matrix of endemic or near-endemic Eastern Arc Mountain amphibian and reptiles species (n = 132) by site, using the Bray–Curtis (Sørensen) similarity index.

This is suggested by the clustering of the Southern Highland site, Rungwe, with Mahenge and Udzungwa. No previous studies exist that suggest the likelihood of this corridor as a potential route for amphibian and reptile species dispersal, but our evidence supports a close faunal similarity between the Mahenge Mountains, Southern Highlands, and Udzungwa Mountains. Interestingly, Rungwe groups with Udzungwa, and this might suggest barriers to dispersal are sufficiently weak between Udzungwa and the Southern Highlands to generate similarity between these faunas. More significant barriers to dispersal are assumed for both the Kilombero Valley (Mahenge-Udzungwa) and the Mbarika Mountains (Southern Highlands–Mahenge) as evidenced by Mahenge's more distinct assemblage in similarity measures. Further testing of these barriers would contribute to our understanding of the biogeographic history of this region of Tanzania. There is some evidence from phylogenetic studies, but this appears to show contrasting patterns. For example Mariaux and Tilbury's (2006) recent study of dwarf chameleons of the genus *Rhampholeon* showed that the nearest relative of *Rhampholeon beraduccii* is *Rhampholeon nchisiensis* of the Southern Highlands. Similarly, populations of *Probreviceps rungwensis* in Mahenge and the Southern Highlands cluster might potentially indicate that this pattern is a general trend. Whether Mahenge, Udzungwa, and Southern Highland faunal similarities can be explained by either dispersal, vicariance, or both patterns will require more comprehensive phylogenetic evidence.

The discovery of a highly diverse forest amphibian and reptile assemblage in a forest fragment of the Eastern Arc Mountains is not unremarkable. Focused survey effort has repeatedly revealed diverse assemblages in the Eastern Arc (e.g., Barbour & Loveridge, 1928; Menegon et al., 2008). Despite the small size of habitats, and often the level of disturbance, these small, ancient forest remnants harbor unique faunal communities (Lovett, 1993). Recent evidence has also suggested that many lineages have long evolutionary histories, presumably due to isolation and long-term persistence of habitats. This finding has further elevated the conservation value of the Eastern Arc Mountains (Burgess et al., 2007). Mahenge can be added as another example of a location showing high amphibian diversity and of high conservation importance.

Comparisons across the Eastern Arc suggest the total forest area is relatively small in Mahenge (see Burgess et al., 2007). Despite the small size of the natural vegetation remnants in Mahenge, species diversity is relatively high. In particular Sali FR, with its broad altitudinal coverage across the montane forest elements, has particularly diverse elements, including several possibly endemic species. The typical montane endemic element associated with the Eastern Arc is mainly restricted to Sali forests above 900 m, including species in the genera *Crotaphopeltis, Hoplophryne, Callulina, Nectophrynoides, Probreviceps, Scolecomorphus,* and *Xyeledontophis,* but absent from Mselezi forests. A taxonomic assessment of the species collected here is required to confirm their taxonomic status, together with focused conservation attention on Sali FR. Assessment of the remaining forest fragments in the Mahenge Mountains might reveal other areas that are equally diverse, and this remains a priority for future work in this area (particularly submontane and montane elements). If current species estimates are correct, Sali FR could rank among the most important forest reserve sites for the conservation of the forest herpetofauna in Eastern Africa. However, further voucher-based research is needed to test this hypothesis.

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Appendix 1

List of Material Collected with K. M. Howell (KMH) Collector Numbers

Amphibians

Arthroleptidae: *Arthroleptis* sp. 1—KMH 26255, 26238–40, 26265, 26267, 26268, 26463, 26636, 26655, 26656, 26983, 26985, 26987; *Arthroleptis lonnbergi*—KMH 26908; *Arthroleptis* cf. *reichei*—KMH 26632, 26633; *Arthroleptis xenodactyloides*—KMH 26253, 26423, 26460, 26642, 26657–60, 26982, 26984, 26988, 26989, 26995; *Leptopelis flavomaculatus*—KMH 26645; *Leptopelis uluguruensis*—KMH 26251, 26258, 26259; *Leptopelis vermiculatus*—KMH 26635, 26964, 26965; **Bufonidae:** *Nectophrynoides* cf. *tornieri*—KMH 26254, 26261, 26262, 26467, 26648, 26652, 26986; *Nectophrynoides* sp. 1—KMH 26252, 26259, 26260, 26263, 26264, 26649, 26650, 26912; *Nectophrynoides* sp. 2—KMH 26637–39, 26641, 26643, 26644, 26988, 26999; *Mertensophryne loveridgei*—KMH 26653; **Hyperoliidae:** *Afrixalus* cf. *uluguruensis*—KMH 26269, 26646, 26950, 26957, 26966, 26992, 26993; *Afrixalus fornasinii*—KMH 26462, 26634, 26952; *Afrixalus* sp. 1—KMH 26958, 26962, 26970, 26971, 26974; *Afrixalus* sp. 2—KMH 26651, 26968, 26980; *Hyperolius* cf. *puncticulatus*—KMH 26956, 26961; *Hyperolius* sp. 1—KMH 26955, 26959, 26960, 26967, 26972, 26976, 26977, 26979, 26996; *Hyperolius* sp. 2—KMH 26951, 26954, 26973, 26977, 26978; **Brevicipitidae:** *Callulina* sp.—KMH 26266, 26911, 26963, 26975; *Probreviceps* sp.—KMH 26256, 26640, 26969, 26991; *Spaelophryne methneri*—KMH 26461, 26990; **Microhylidae:** *Hoplophryne* sp.—KMH 26981; **Petropedetidae:** *Petropedetes* sp.—KMH 26242–50, 26419, 26420, 26907; **Phrynobatrachidae:** *Phrynobatrachus natalensis*—KMH 26422, 26459, 26654; *Phrynobatrachus acridoides*—KMH 26421, 26458; *Phrynobatrachus uzungwensis*—KMH 26241, 26953, 26994.

Additional specimen records in Loader et al., 2004.

Reptiles

Gekkonidae: *Cnemaspis* sp.—KMH 23945, 23946, 26756, 26757, 26762, 26767, 26768, 26772; **Scincidae:** *Melanoseps loveridgei*—KMH 23948, 26765, 26771, 26774; Trachylepis striata—KMH 26769; **Chamaeleonidae:** *Rhampholeon beraduccii*—KMH 26752, 26754, 26758, 26759, 26775; *Rieppeleon brevicaudatus*—KMH 23947, 26753, 26760; **Colubridae:** *Crotaphopeltis tornieri*—KMH 26781, 26763; *Crotaphopeltis hotamboeia*—KMH 26782, 26784; *Dasypeltis medici*—KMH 26780; *Lycodonomorphus whytei*—KMH 26773; *Natriciteres sylvatica*—KMH 26418, 26783; *Philothamnus semivariegatus*—KMH 23949; *Philothamnus* cf. *angolensis*—KMH 26417, 26779; *Philothamnus hoplogaster*—KMH 26416; *Psammophis orientalis*—KMH 26785; *Thelotornis mossambicanus*—KMH 26778; *Xyeledontophis* cf. *uluguruensis*—KMH 26755; **Lamprophiidae:** *Atractaspis aterrima*—KMH 26764; *Lamprophis* cf. *fuliginosus*—KMH 26766; **Viperidae:** *Causus defilippii*—KMH 26776, 26777.

Additional specimen records in Loader et al., 2004.

Chapter 9

Herpetofauna of Montane Areas of Tanzania. 5. Range Extension of *Phrynobatrachus sulfureogularis* (Anura, Phrynobatrachidae) from Burundi to the Mahale Mountains of Western Tanzania with a Redescription of the Species

Lucinda P. Lawson[1] and Breda Zimkus[2]

[1]*Department of Zoology, Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, IL 60605, USA*
[2]*Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138, USA*

Abstract

Two large forest *Phrynobatrachus* (male, snout–urostyle length 42.2 mm; subadult, snout–urostyle length 27.4 mm) were collected from the Mahale Mountains in Tanzania, exhibiting a large tympanum (55%–76% of the eye diameter), large digital discs, and a bright yellow throat in males. A comparison of these two individuals with all described *Phrynobatrachus* species was made, and they were found to fit the description of *P. sulfureogularis*, a poorly known species only known from the type locality in Burundi. This new population represents a substantial southern range extension or potentially a similar, yet undescribed species.

Introduction

Phrynobatrachus sulfureogularis Laurent, 1951, is a large species (snout–vent length [SVL] up to 43 mm) of puddle frog, known previously only from the type locality in Nanzergwa, Burundi, at 2300–2500 m (Fig. 1). *Phrynobatrachus sulfureogularis* is characterized by its granular dorsum, moderate to extensive pedal webbing, and greatly expanded digital discs. Breeding males exhibit a yellow gular region and minute asperities, particularly on the posterior hind limbs and the latero-ventral part of toe V.

Two large *Phrynobatrachus* specimens (male, snout–urostyle length [SUL] = 42.2 mm; juvenile, SUL = 27.4 mm) were recently collected from Mahale Mountains (Fig. 1) in western Tanzania by W. Stanley (FMNH 275459 and 275460) that exhibited many of the morphological characteristics of *P. sulfureogularis*. Comparisons of the individuals from Mahale (*P.* cf. *sulfureogularis*) were made to other puddle frog species distributed in Tanzania, Burundi, Rwanda, and the eastern Democratic Republic of the Congo. The new specimens were then compared with the type series of *P. sulfureogularis* (by B.Z.) at the Royal Museum for Central Africa (Tervuren, Belgium) to determine whether the new collections were conspecific with the type series.

In the original description by Laurent (1951), the type specimen (female) was described, and the existence of 20 paratypes was recorded. The description lacked any morphometric data and was vague on many key details. *Phrynobatrachus sulfureogularis* is herewith redescribed and compared with specimens from the Mahale population.

Methods

Both individuals from the Mahale population of *P. sulfureogularis* were caught by hand along a small river 0.5 km northwest of Nkungwe Hill Summit, 6.10343°S, 29.77895°E, 2100 m, on 25 August 2003 (FMNH 275459) and 27 August 2003 (FMNH 275460) by W. Stanley. The Mahale specimens were collected incidentally, and neither detailed habitat nor call data were taken. Measurements taken on preserved specimens are SUL, head length (HDL), head width (HDW), width of the eye at its widest point (EYE), width of the interorbital space (IOS), width of the internarial space (INS), distance between the eye and the naris (ENS), distance between the naris and the tip of the snout (NS), distance between the naris and the edge of the upper lip (NLL), tibia–fibula length (TiL), femur length (FeL), tarsus length (TaL), distance between the inner and outer metatarsal tubercles (IOMT), width of the hand at its widest point (HaW), distance between the base of the hand and the tip of the third finger (FiL3), tympanum width (Tym), and length of the first toe (ToL1) and fourth toe (ToL4). Webbing formula reflects the extent of the main, broad web as opposed to the more variable thin fringe on the toes.

The type series from the Royal Museum for Central Africa (RMCA) was examined by B.Z., with particular focus on male specimens comparable to the specimens from Mahale. Paratype specimens were originally grouped within the series RMCA B.108822–108841 but not assigned individual numbers. All those identified as mature males and females were assigned museum catalogue numbers RMCA B.108821

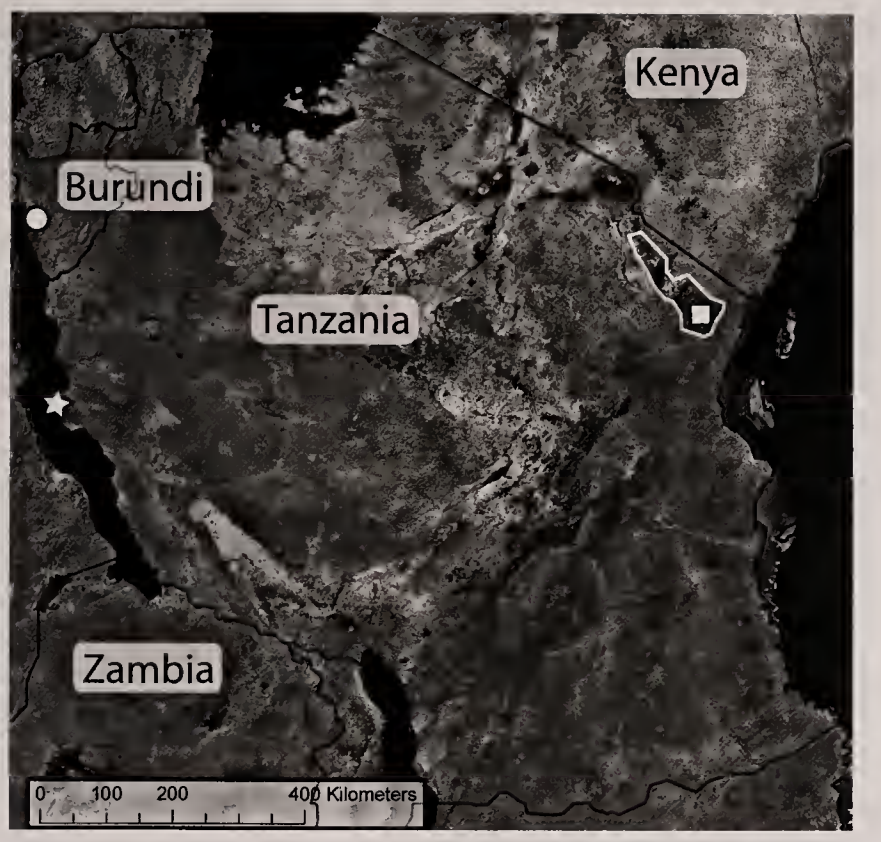

FIG. 1. Type locality of *P. sulfureogularis* (circle), new locality of *P.* cf. *sulfureogularis* (star), type locality of *P. krefftii* (square), and known distribution of *P. krefftii* (outlined area).

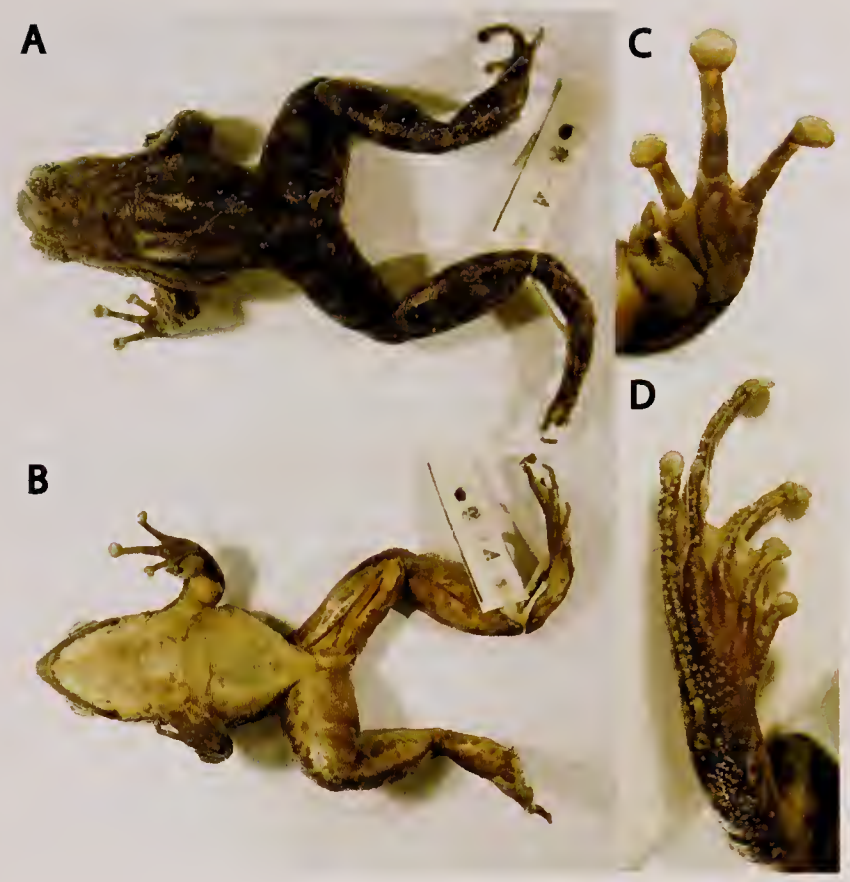

FIG. 2. Photographs of *P.* cf. *sulfureogularis* (FMNH 275460) from Mahale, Tanzania. Dorsal view (**A**), ventral view (**B**), detail of ventral side of hand, showing expanded digital discs and nuptial pad on the base of finger I (**C**), detail of ventral side of foot (**D**).

through RMCA B.108829. The female holotype and three breeding males were subsequently photographed and measured (female type = RMCA B.108821, male paratypes = RMCA B.108822, RMCA B.108823, and RMCA B.108824) as described above. In addition to those specimens that had complete morphometric data measured, SUL data were obtained from five additional mature males and one female to determine the overall size range within the series.

Results

Description of Specimens (*P.* cf. *sulfureogularis*) from Mahale

Measurements from representatives of the Burundi type series and the Mahale series are displayed in Table 1. Only one of the two Mahale specimens (both male) appears to be an adult, with a SUL of 42.2 mm. The snout is elongated, sharp, and noticeably overhangs the lower jaw; a small, oval papilla present on the tongue; canthus rostralis rounded; tympanum is large, round, and approximately 75% the size of the eye; minimal supratympanic ridge; eye width is greater than tympanum diameter and greater than the interobital space; eyes have horizontal pupils that are visible from below; manual webbing absent; internarial distance is equal or less than the interorbital distance; round nostrils visible from above; nostrils closer to the snout tip than the eye and have a slightly raised ridge on outside; tibia is approximately 50% of the snout–vent length; femur is approximately 50% of the snout–vent length; tibio-tarsal articulation reaches the eye; finger and toe tips are expanded into large discs (Fig. 2); manual webbing is absent; subarticular tubercles are well defined; second finger is longer than the first; third finger is 28% of the snout–vent length; inner metatarsal tubercle oval-shaped; outer metatarsal and tarsal tubercles round; toe-webbing formula: 1 (disc), 2i (1st), 2e (disc), 3i (1.75), 3e (2nd), 4i (2nd), 4e (2nd), 5 (1.5); dorsal skin very finely granular with small, round asperities on the lower back and legs; two oblique glandular folds often present in the scapular region of the dorsum, followed in the lumbar area by a semi-circular fold with posterior concavity that is sometimes broken; femoral glands absent; gular sac with lateral vocal folds running parallel to the jaw line; minute spinules present in males, particularly on the posterior limbs and the lateroventral part of toe V. Dorsal and ventral views, along with details of the foot and hand, are shown in Figure 2.

Dorsal coloration dark brown with darker speckles; glandular folds often darker; ventral surface light in color (in alcohol), throat in males bright yellow in life (Fig. 3). Light speckling across pectoral region; upper jaw mottled; indistinct light eye-to-arm band present above the tympanum; anterior surface of the thigh and posterior surface of the tibia banded; posterior surface of the thigh speckled or banded.

Redescription of *P. sulfureogularis*

Phrynobatrachus sulfureogularis was first described by Laurent (1951), based on a type series collected from the Nanzergwa Massif in Burundi (2300–2500 m, −3.4°S, 29.5°E). The type series is the only known collection of *P. sulfureogularis* and is housed in the RMCA Tervuren, Belgium. This species appears to have escaped further scientific inquiry until the present study.

Laurent (1951) described *P. sulfureogularis* as an exceptionally large *Plurynobatrachus* with a distinctive yellow vocal sac. The following three paragraphs are a translation from the type description, confirmed by examination of the type series by Zimkus.

Specimens of *P. sulfureogularis* possess both a distinct canthus rostralis and a slightly concave frenal region. Toes are

TABLE 1. Measurements (in mm) of two specimens of *Phrynobatrachus* cf. *sulfureogularis* (male and juvenile: Mahale, Tanzania), type specimen of *P. sulfureogularis* (female: Burundi), and two paratypes (males: Burundi).

	Mahale (male) FMNH 275460	Mahale (juvenile) FMNH 275459	Holotype (female) RMCA B108821	Paratype (male) RMCA B108822	Paratype (male) RMCA B108823	Paratype (male) RMCA B108824
SUL	42.2	27.4	42.2	40.4	38.3	36.8
HDL	14.6	10.3	16.9	15.2	16.0	13.5
HDW	13.5	9.6	14.4	12.6	13.4	12.9
EYE	4.65	3.6	5.4	5.6	4.9	5.2
IOS	3.9	2.8	4.1	4.6	4.0	3.9
INS	3.9	2.7	3.9	3.9	3.7	3.8
ENS	3.2	2.3	3.4	3.0	2.9	2.5
NS	2.2	1.7	1.5	1.7	2.2	2.1
NLL	2.6	1.8	2.6	2.6	2.4	1.9
TiL	20.7	13.8	21.1	22.5	22.0	20.1
FeL	21.0	12.6	18.8	20.1	19.5	17.6
TaL	11.1	6.8	—	—	—	—
IOMT	2.1	1.7	2.0	2.3	2.6	2.1
ToL4	21.3	13.7	17.6	18.5	18.0	—
ToL1	7.1	6.2	5.1	6.0	5.4	—
HaW	4.6	3.2	5.0	6.0	4.8	4.9
FiL3	11.7	7.4	13.3	12.3	11.6	10.2
Tym	3.5	2.0	3.2	3.9	3.5	3.5

two-thirds webbed, deeply penetrating the webbing between the metatarsals, and sub-articular tubercles are prominent. The tibio-tarsal articulation reaches the eye. The skin is finely granular with spiny dorsal-lateral folds in males. In many specimens from the type series, two converging oblique glandular folds extend to the shoulder region, followed in the lumbar region by a semi-circle concave posterior fold.

The dorsal coloration is brownish, blackish olive, and speckled with a darker flecks. The glandular folds are sometimes darker than the surrounding skin. Transverse bands are distinct on the anterior thighs and shins, in a low proportion of specimens (both male and female: 3/20). In some specimens, two clear dorsolateral stripes are present, similar to those often observed in *P. acutirostris*, *P. versicolor,* and *P. dendrobates*.

The ventral surface is cream with diffuse darker pigmentation around the legs and throat in females. In males, legs and chest are distinctly darkly pigmented, creating a sharp contrast to the rest of the ventral surface. The vocal sac of the male is bright sulfur-yellow with lateral folds. The spiny tubercles of the male are particularly numerous on the hind limbs and the ventral lateral part of the fifth toe.

In addition to translating the type description (presented above), we measured a number of paratypes and recorded traits not mentioned in the original (measurements in Table 1). The conical papilla in the middle of the tongue is large and distinct. The snout is more rounded in some (e.g., males RMCA 108822, 108824) and pointed in others (e.g., males RMCA 108823), always distinctly overhanging the lower jaw. The tympanum is distinct and smaller than the eye width. Specimens possess a glandular fold starting behind the eye, passing over the tympanum and extending to the birth of the forelimb. Nostrils are slightly closer to the end of the snout than to the eye, although variable. In addition to the female holotype, for which the SVL

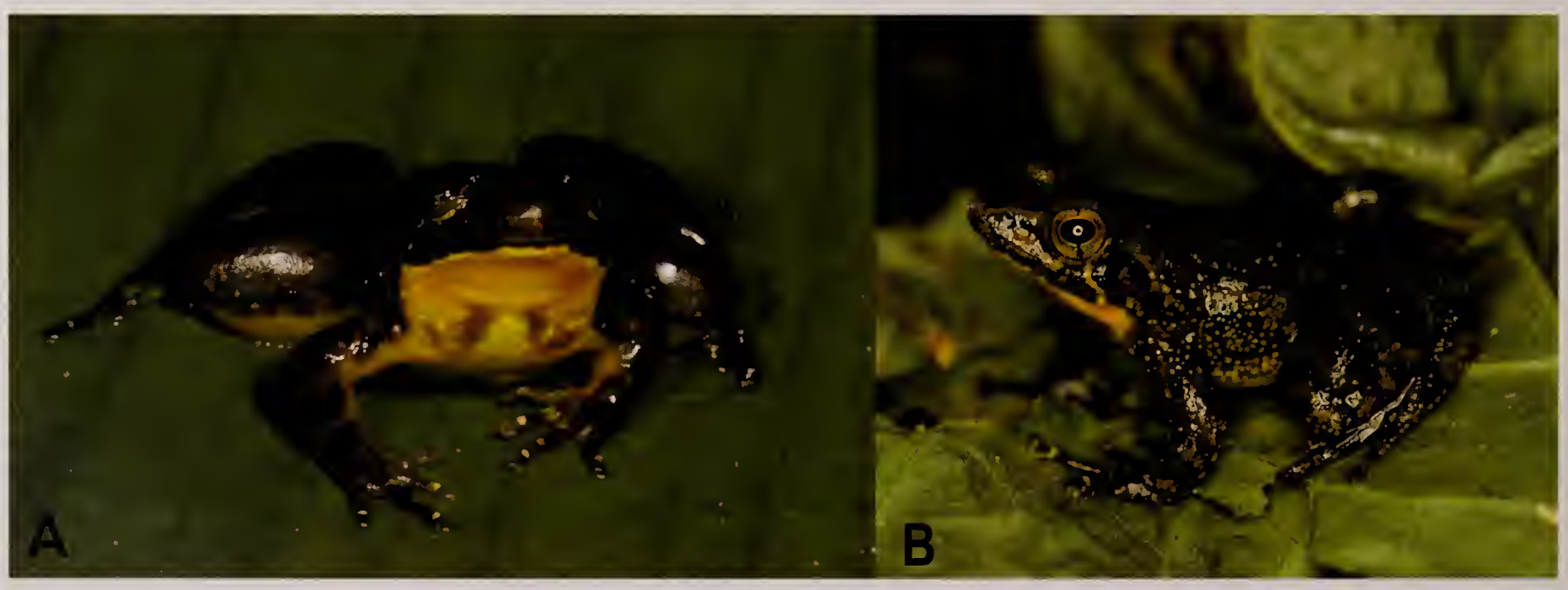

FIG. 3. Photographs of *Phrynobatrachus krefftii* (**A**) and *P.* cf. *sulfureogularis* (**B**) males in life, illustrating bright yellow throat. *Phrynobatrachus krefftii* photo by D. L. Mahler and B. Zimkus; *P.* cf. *sulfureogularis* Mahale specimen photo by W. Stanley.

measured 42.2 mm, the largest female paratype measured 43.6 mm. Males from Burundi had a maximum SVL of 42.6 mm (n = 8).

From the morphological comparison of the new specimens (measurements in Table 1) to the type series, we believe that the population of large-bodied, yellow-throated *Phrynobatrachus* from Mahale cannot be definitively excluded from *P. sulfureogularis* based on any trait described above. Because of the high rate of endemism seen in this area, the isolation between the localities, and the limited sample size of the new population, we will refer to this population as *P.* cf. *sulfureogularis* until larger sample sizes, call data, and molecular data are available to clarify these relationships. The new population can be easily distinguished from all other *Phrynobatrachus* species, however. Because both share the traits described below, we collectively refer to them as *P. sulfureogularis* in comparisons.

Comparisons

The large size of *P. sulfureogularis* distinguishes this puddle frog from most of the species of the genus, and a number of additional morphological characteristics also reveal the distinctness of this form. The clearly visible and large tympanum, as well as the large size, distinguish it from a number of species distributed in Burundi and Tanzania, including *P. acridoides, P. breviceps, P. keniensis, P. mababiensis, P. pakenhami, P. pallidus, P. parvulus, P. rouxi, P. rungwensis, P. scheffleri, P. stewartae, P. ukingensis, P. ungujae,* and *P. uzungwensis.* The tympanum of *P. perpalmatus* is only feebly distinct, and this small species (SVL < 29 mm) exhibits only slightly swollen digit tips. *Phrynobatrachus bullans* exhibits a visible tympanum and moderate webbing on the toes but lacks digital discs, has a grey or brown dorsum, and is significantly smaller (SVL < 28 mm) than *P. sulfureogularis.* The tympanum may or may not be visible in *P. natalensis*, which also exhibits pedal moderate webbing, but this species is also significantly smaller in size (SVL < 31 mm) when compared with *P. sulfureogularis.* A distinct tympanum and moderate pedal webbing characterize *Phrynobatrachus bequaerti*, but digit tips are only slightly expanded, and size is significantly smaller (SVL < 25 mm).

Phrynobatrachus sulfureogularis is morphologically most similar to *P. acutirostris, P. asper, P. dendrobates*, *P. irangi*, *P. petropedetoides*, *P. versicolor*, and *P. krefftii. Phrynobatrachus acutirostris* differs from *P. sulfureogularis* by its conical rather than oval papilla on the tongue, eye length less than interorbital space, smaller digital discs, smooth as opposed to granular skin, and venter that is mottled, speckled, or dotted, often with a longitudinal band running through the throat and breast. *Phrynobatrachus asper* differs from *P. sulfureogularis* by its blunt digital tips and absence of discs, numerous longitudinal folds and rows of warts and tubercles on the dorsum, and extensive pedal webbing with between one and two phalanges free on toe IV (compared with *P. sulfureogularis* with two phalanges free on toe IV). The eye to nostril distance is also greater than nostril to snout distance in *P. sulfureogularis* (1.45–1.35 mm), whereas the nostril is located midway between the eye and the tip of the snout in *P. asper. Phrynobatrachus dendrobates* and *P. petropedetoides* can be easily distinguished from *P. sulfureogularis* by their blunter snouts (compared with the protruding and sharply pointed profile of *P. sulfureogularis*), conical rather than oval papillae on the tongue, less extensive pedal webbing with three phalanges free on toe IV, and eye width greater than interorbital space. *Phrynobatrachus irangi* differs from *P. sulfureogularis* by its moderate webbing with three phalanges free on toe IV, digital tips that are rounded and only slightly dilated, and a gular region that is somewhat grayish. *Phrynobatrachus versicolor* differs from *P. sulfureogularis* because toe discs are less developed in the former, a more or less distinct median line may be present on the venter, the interorbital space is broader than upper eyelid, and the nostril is located midway between the eye and the tip of the snout.

Only five species of *Phrynobatrachus* exhibit a bright yellow throat in breeding males: *P. sulfureogularis, P. krefftii, P. latifrons, P. minutus*, and *P. alleni. Phrynobatrachus alleni* and *P. latifrons*, found in West Africa, and *P. minutus*, found in Ethiopia, are all much smaller than *P. sulfureogularis* and the Mahale specimens (*P. alleni* males average 18.4 mm SUL [Rödel & Ernst, 2002], *P. latifrons* males average 14–20 mm [Rödel, 2000], and *P. minutus* males average 15–20 mm [Boulenger, 1895]). *Phrynobatrachus latifrons* and *P. minutus* both have small tympanums and lack true discs (Rödel, 2000), unlike *P. sulfureogularis* and the Mahale specimens.

Phrynobatrachus sulfureogularis is most notably similar to *P. krefftii*, particularly regarding its size and bright yellow throat in breeding males (Fig. 3). Snout–vent lengths of *P. krefftii* range from 36 to 46 mm (n = 14) in males and 45 to 51 mm (n = 4) in females (Drewes & Perret, 2000). Many additional characteristics are similar, including similar dorsal and ventral markings (light and dark brown mottling on the dorsal and lateral surfaces, light and dark brown banding on the hind legs, and light lines on the fingers at the base of the expanded disks), large expanded disks on fingers and toes, and presence of thickened nuptial pads on base of finger I in males. Extent of pedal webbing is similar between the two species with one or two phalanges free on toe IV (Channing & Howell, 2006; Pickersgill, 2007), and the tympanum is 75% of eye width in *P. sulfureogularis*, within the 60%–80% range in *P. krefftii.* A number of characteristics differentiate *P. krefftii* from *P. sulfureogularis*; a conical rather than oval papilla is present on the tongue of the former, interorbital space as broad as the upper eyelid (compared with eye width that is greater than interobital space in *P. sulfureogularis*), toe discs are smaller and often have a terminal point in *P. krefftii* when compared with *P. sulfureogularis*, and lack of asperities on the plantar surface of the foot, although plantar spines are present on the toes. Although similar, it appears that the overall shape of *P. sulfureogularis* is different from *P. krefftii* (measurement for *P. krefftii* from Pickersgill, 2007); head width/SVL = 32%, slightly smaller than the 34%–40% (mean 37%) for *P. krefftii*; tibia/SVL = 49%, compared with the 50%–55% (mean 52%) for *P. krefftii*: head width/tibia = 65%, compared with 68%–75% (mean 71%) in *P. krefftii.*

Phrynobatrachus krefftii is known from the Eastern Arc Mountains of Tanzania, specifically from the East and West Usambara Mountains (Fig. 1). Descriptions for comparisons were taken from Boulenger (1919), De Witte (1941), Laurent (1941, 1951, 1972), Grandison and Howell (1983), Poynton and Broadley (1985), Drewes and Perret (2000), Rödel (2000), Rödel & Ernst (2002), Crutsinger et al. (2004), Hirschmann and Hödl (2006), and Pickersgill (2007).

Discussion

Species delimitation of African herpetofauna can be a difficult task, confounded by vague type descriptions, absence of molecular data for type specimens, and generally poor sampling. It was difficult initially to identify *P.* cf. *sulfureogularis* collected from Mahale National Park in Tanzania as being previously described or distinct and new due to lack of documentation on *P. sulfureogularis*. For example, *P. sulfureogularis* is not mentioned among the yellow-throated *Phrynobatrachus* in Hirschmann and Hödl's (2006) recent study, and this information was only available in the original description by Laurent (1951). Although morphologically similar to the type series of *P. sulfureogularis*, the taxonomic distinctiveness of the populations of *P.* cf. *sulfureogularis* should be assessed in the future. This aspect is highlighted because of the distance of approximately 300 km between Tanzanian and Burundi populations and the distinctiveness of mountain assemblages and high rates of endemism across this region (Fjeldså, 2003). Examination and description of live specimens, including call recordings, DNA analysis, and ecological information of both populations is necessary to clarify the relationship between *P. sulfureogularis and P.* cf. *sulfureogularis,* and between these and other *Phrynobatrachus* species. No genetic data currently exist for *P. sulfureogularis*, but due to appearance and geographic distribution, Zimkus et al. (2010) hypothesize that this species would fall within the clade known to contain *P. krefftii* and the Albertine Rift species *P. acutirostis*, *P. dendrobates, P. petropedetoides*, and *P. versicolor*. Obtaining information from both the type locality and the Mahale population will help to resolve these relationships.

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Field Museum of Natural History
1400 South Lake Shore Drive
Chicago, Illinois 60605-2496